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COMPARATIVE PALEONTOLOGY AND STRATIGRAPHY OF VALANGINIAN POLYPTYCHITINAE AND SIMBIRSKITINAE IN SVERDRUP BASIN (ARCTIC CANADA) AND LOWER SAXONY BASIN (NORTHWEST GERMANY)

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Preface

Correlation of rock units is essential for interpreting the geological history of large regions and paleontology provides one of the most incisive tools for establishing the time relationships amongst sedimentary rocks. The results presented in this bulletin provide much information needed to interpret the history of the Sverdrup Basin of Arctic Canada, an area of considerable interest for hydrocarbon exploration.

This report is the result of close collaboration between Dr. J.A. Jeletzky of the Geological Survey of Canada who for nearly 40 years has studied the Cretaceous of Northern Canada and Dr. E. Kemper of the Bundesanstalt fuer Geowissenschaften und Rohstoffe of the Federal German Republic, a leading authority on the Cretaceous of northwestern Germany. These authors with the assistance of many colleagues have brought together information from many sources and in many languages concerning the early Lower Cretaceous of the Boreal Realm.

The result of this collaborative work is a reinterpretation of previously described and critical fossil species with particular reference to Canadian material. Equally important results of the study pertaining to the German material are being published elsewhere by Dr. Kemper.

The importance attached to studies of such Cretaceous fauna is shown by the veritable flood of Soviet publications dealing with material for Valanginian fauna from North Siberia that was received by the authors soon after the final manuscript had been completed.

This report contributes to an ongoing objective of the Geological Survey — the expansion of the geoscience knowledge base available to Canada. This pool of information is fundamental to any geoscience activities whether done by industry or for government.

Ottawa

R.A. Price
Assistant Deputy Minister,
Geological Survey of Canada

Préface

La corrélation d'unités lithologiques est essentielle pour l'interprétation de l'évolution géologique des régions étendues, et la paléontologie représente l'un des outils les plus utiles à l'établissement des liens chronologiques qui existent entre les roches sédimentaires. Le présent bulletin fournit une bonne partie des données requises pour l'interprétation de l'évolution du bassin de Sverdrup dans l'Arctique canadien, zone fort intéressante en matière d'exploration des hydrocarbures.

Ce rapport est la résultat d'une étroite collaboration entre MM. J.A. Jeletzky de la Commission géologique du Canada, qui étudie le Crétacé du Nord du Canada depuis près de quarante ans, et E. Kemper, un expert en matière du Crétacé de l'Allemagne du Nord-Ouest, qui est au service du Bundesanstalt fuer Geowissenschaften und Rohstoffe de la République fédérale d'Allemagne. Les auteurs, avec l'aide d'un grand nombre de collègues, ont rassemblé des données, tirées de nombreuses sources et dans une gamme de langues, sur le début du Crétacé inférieur du royaume arctique.

Ces travaux de nature collaborative ont permis de réinterpréter, en fonction du matériel canadien, des espèces fossiles essentielles déjà décrites. Les résultats tout aussi importants de l'étude qui ont trait au matériel allemand seront publiés ailleurs par M. Kemper.

L'avalanche de publications russes portant sur les faunes valanginiennes de la Sibérie septentrionale adressée aux auteurs depuis l'achèvement du manuscrit définitif témoigne de l'importance accordée aux études de ces faunes crétacées.

Le rapport contribue à la réalisation d'un objectif permanent de la Commission géologique du Canada, soit d'élargir la base de données géoscientifiques qui existe au Canada. Ce réservoir d'information est essentiel à toutes les activités géoscientifiques, qu'elles soient entreprises par l'industrie ou à l'intention du gouvernement.

Ottawa

Le sous-ministre adjoint
de la Commission géologique du Canada

R.A. Price

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COMPARATIVE PALEONTOLOGY AND STRATIGRAPHY OF VALANGINIAN POLYPTYCHITINAE AND SIMBIRSKITINAE IN SVERDRUP BASIN (ARCTIC CANADA) AND LOWER SAXONY BASIN (NORTHWEST GERMANY).

Abstract

A comparative paleontological and stratigraphical study of the Valanginian Polyptychitinae and Simbirskitinae of the Sverdrup and Lower Saxony basins confirmed the idea that the Lower Saxony Basin was the principal evolutionary centre of Polyptychitinae. However, it has also demonstrated the existence of important additional evolutionary centres of Polyptychitinae in the high Boreal Valanginian basins, particularly in Central Siberia and Sverdrup Basin. The relatively rare polyptychitinid migrants from the Lower Saxony Basin experienced a considerable endemic evolution in these two high Boreal basins, which produced a considerable number of local polyptychitinid taxa (e.g. Astieriptychites, Siberiptychites *s. str.,* Pseudoeuryptychites, *and* Amundiptychites*) and the late Valanginian Simbirskitinae (e.g.* Ringnesiceras*). These endemic high Boreal offsprings were the principal inhabitants of the high Boreal seas of Eurasia and North America while the bulk of the Lower Saxonian polyptychitinids remained confined to the Subboreal seas of Northwestern and Central Europe. Polyptychitinae conspecific, and even congeneric, with those of the Lower Saxony Basin and other marginal Boreal basins of Europe are rather rare in the high Boreal (or Arctic) Valanginian basins. Furthermore, they appear to be confined to a few restricted stratigraphic levels (e.g. closely above the Berriasian/Valanginian boundary and at or near the lower/upper Valanginian boundary) apparently coincidental with transgressional maxima that facilitated the "escapes" of the European polyptychitinids into the high Arctic basins.*

The following Lower Saxonian and related European polyptychitinid taxa are described and figured: genus Peregrinoceras *Sazonova sensu Casey 1973; genus* Bodylevskites *Klimova with* P. pumilio *(Vogel); genus* Paratollia *Casey with* P. kemperi *Casey,* P. *cf.* kemperi *Casey,* P. emslandensis *(Kemper),* P. *aff.* emslandensis *(Kemper), and* P. tenuicostata *(Kemper); genus* Euryptychites *Pavlow 1914 with* E. *latissimus (Neumayr and Uhlig),* E. diplotomus *(Koenen), and* E. *aff.* laevis *Donovan; genus* Neocraspedites *Spath with* N. semilaevis *(Koenen),* N. *n.sp. aff.* semilaevis *(Koenen),* N. greenlandicus *(Donovan),* N. semisulcatus *(Koenen) and* N. undulatocostatus *(Donovan); genus* Propolyptychites *Kemper with* P. quadrifidus *(Koenen) and* P. bentheimensis *Kemper; genus* Polyptychites *Pavlow with* P. polyptychus *(Keyserling),* P. michalskii *(Bogoslovsky),* P. oerlinghusanus *(Weerth),* P. pavlowi *Koenen,* P. brancoi *(Neumayr and Uhlig),* P. lamplughi *Pavlow,* P. keyserlingi *(Neumayr and Uhlig),* P. ascendens *Koenen,* P. ramulicosta *Pavlow,* P. *aff.* keyserlingi *(Neumayr and Uhlig),* P. multicostatus *Koenen,* P. clarkei *Koenen,* P. orbitatus *Koenen,* P. saxonicus *n. sp.,* P. tethyale *n. sp.,* P. sublatissimus *Spath,* P. sphaeroidalis *Koenen,* P. hapkei *n. sp.,* P. triplodiptychus *Pavlow,* P. villersensis *Baumberger,* P. multiplicatus *Roemer; genus* Hollwediceras *n. genus with* H. sphaericus *(Koenen); genus* Prodichotomites *Kemper with* P. polytomus *(Koenen),* P. hollwedensis *Kemper,* P. pfaffi *n. sp.,* P. robustus *n. sp.,* P. flexicosta *(Koenen),* P. complanatus *(Koenen),* P. fissuratus *(Koenen),* P. undulatus *(Koenen),* P. glaber *n. sp.,* P. perovalis *(Koenen),* P. ivanovi *(Aristov) and* P. grotriani *(Neumayr and Uhlig).*

The following polyptychitinid taxa are described and figured from the Sverdrup Basin and other high Boreal (or high Arctic) basins: genus Polyptychites *with* P. keyserlingi *(Neumayr and Unlig),* P. *aff.* hapkei *n. sp.,* P. tschekanovskii *Pavlow,* P. *aff.* tschekanovskii *Pavlow,* Polyptychites *n. sp. A,* P. canadensis *Kemper and Jeletzky,* P. balkwilli *n. sp.,* Prodichotomites *aff.* hollwedensis *Kemper; genus* Siberiptychites *including the subgenus* Siberiptychites *s. str. with* S. *(S.)* stubendorffi *(Schmidt),* S. *(S.) n. sp. aff.* stubendorffi *(Schmidt),* S. *(S.)* fascicostatus *n. sp.; subgenus* Pseudoeuryptychites *Jeletzky 1986 with* S. *(P.)* middendorffi *(Pavlow),* S. *(P.) cf. or aff.* middendorffi *(Pavlow),* S. *(P.)* pavlovi *(Voronets),* S. *(P.)* pateraeformis *(Voronets),* S. *(*Pseudoeuryptychites*) n. sp. indet. A; and* Siberiptychites *(new subgenus)? n. sp. B; genus* Astieriptychites *Bodylevsky with* A. obsoletus sp. nov., A. sp. indet. A, *and* A? sp. indet. B.; *genus* Amundiptychites *Kemper and Jeletzky with* A. sverdrupi *Kemper and Jeletzky,* A. *aff.* sverdrupi *Kemper and Jeletzky,* A. thorsteinssoni *n. sp., and* A. fasciatus *n. sp. Also described and figured are the following late Valanginian taxa of Simbirskitinae Spath; genus* Ringnesiceras *Kemper and Jeletzky including the sub-*

genus Ringnesiceras *s. str. with* R. (R.) amundense *Kemper and Jeletzky*, R. (R.) pseudopolyptychum *Kemper and Jeletzky*, R. (R.) tozeri *Kemper and Jeletzky, and* ?R. (R.) *n. sp. aff.* amundense *Kemper and Jeletzky and subgenus* Elleficeras *Kemper and Jeletzky with* R. (E.) ellefense *Kemper and Jeletzky and* R. (E.) *n. sp. indet.*

The Valanginian generation of the Lower Saxony Basin was situated near the boundary of the Boreal and Tethyan faunal realms and had easy marine connections with both. Therefore, the basin contains an appreciable admixture of the diagnostic Tethyan ammonites. At the same time some of its diagnostic polyptychitinids migrated northward into the high Boreal basins of Eurasia and North America. Therefore, Valanginian ammonite faunas of the Lower Saxony Basin are extremely important for the zonal correlation of the Tethyan Valanginian rocks with their marginal Boreal and high Boreal equivalents. A new scheme of a zonal correlation of the Valanginian rocks of the Sverdrup Basin with those of Central Siberia, Lower Saxony Basin, and the Vocontian Trough is proposed.

Résumé

Une étude comparative de la paléontologie et de la stratigraphie des Polyptychitinae et des Simbirskitinae valanginiens des bassins de Sverdrup et de la Basse-Saxe a confirmé l'hypothèse selon laquelle le bassin de la Basse-Saxe aurait été le principal centre d'évolution des Polyptychitinae. L'étude a également démontré l'existence d'autres grands centres d'évolution des Polyptychitinae dans les bassins arctiques d'âge valanginien de Sibérie centrale et de Sverdrup. Les assez rares polyptychitinidés qui se sont échappés du bassin de la Basse-Saxe ont subi une évolution endémique considérable dans ces deux bassins arctiques, laquelle a produit un grand nombre de taxons de polyptychitinidés de caractère régional (p. ex., Astieriptychites, Siberiptychites s. str., Pseudoeuryptychites *et* Amundiptychites*) ainsi que les Simbirskitinae datant du Valanginien supérieur (p. ex.,* Ringnesiceras*). Ces descendants endémiques d'origine arctique ont peuplé les mers arctiques de l'Eurasie et de l'Amérique du Nord, tandis que la plupart des polyptychitinidés de la Basse-Saxe sont demeurés dans les mers subarctiques de l'Europe du Nord-Ouest et de l'Europe centrale. Les polyptychitinidés appartenant aux mêmes espèces aussi bien qu'aux mêmes genres que ceux du bassin de la Basse-Saxe et d'autres bassins subarctiques d'Europe sont relativement rares dans les bassins arctiques d'âge valanginien. En outre, ces organismes ne semblent se manifester qu'à quelques niveaux stratigraphiques restreints (p. ex., juste au-dessus de la limite du Berriasien et du Valanginien et à la limite du Valanginien inférieur et du Valanginien supérieur, ou près de celle-ci), coincidant avec des transgressions maximales qui ont facilité la migration des polyptychitinidés européens dans les bassins de l'Extrême-Arctique.*

Le présent bulletin fait état, au moyen de descriptions et d'illustrations, des taxons suivants de polyptychitinidés de la Basse-Saxe et d'autres régions d'Europe: le genre Peregrinoceras *Sazonova sensu Casey 1973; le genre* Bodylevskites *Klimova, avec* P. pumilio *(Vogel); le genre* Paratollia *Casey, avec* P. kemperi *Casey*, P. *cf.* kemperi *Casey*, P. emslandensis *(Kemper)*, P. *aff.* emslandensis *(Kemper) et* P. tenuicostata *(Kemper); le genre* Euryptychites *Pavlow 1914, avec* E. latissimus *(Neumayr et Uhlig)*, E. diplotomus *(Koenen) et* E. *aff.* laevis *Donovan; le genre* Neocraspedites *Spath, avec* N. semilaevis *(Koenen)*, N. greenlandicus *(Donovan)*, N. semisulcatus *(Koenen) et* N. undulatocostatus *(Donovan); le genre* Propolyptychites *Kemper, avec* P. quadrifidus *(Koenen), et* P. bentheimensis *Kemper; le genre* Polyptychites *Pavlow, avec* P. polyptychus *(Keyserling)*, P. michalskii *(Bogoslovsky)*, P. oerlinghusanus *(Weerth)*, P. pavlowi *Koenen*, P. brancoi *(Neumayr et Uhlig)*, P. lamplughi *Pavlow*, P. keyserlingi *(Neumayr et Uhlig)*, P. ascendens *Koenen*, P. ramulicosta *Pavlow*, P. *aff.* keyserlingi *(Neumayr et Uhlig)*, P. multicostatus *Koenen*, P. clarkei *Koenen*, P. orbitatus *Koenen*, P. saxonicus *nouv. esp.*, P. tethyale *nouv. esp.*, P. sublatissimus *Spath*, P. sphaeroidalis *Koenen*, P. hapkei *nouv. esp.* P. triplodiptychus *Pavlow*, P. villersensis *Baumberger*, P. multiplicatus *Roemer; le genre* Hollwediceras *nouv. genre, avec* H. sphaericus *(Koenen); le genre* Prodichotomites *Kemper, avec* P. polytomus *(Koenen)*, P. hollwedensis *Kemper*, P. pfaffi *nouv. esp.*, P. robustus *nouv. esp.*, P. flexicosta *(Koenen)*, P. complanatus *(Koenen)*, P. fissuratus *(Koenen)*, P. undulatus *(Koenen)*, P. glaber *nouv. esp.*, P. perovalis *(Koenen)*, P. ivanovi *(Aristov) et* P. grotriani *(Neumayr et Uhlig).*

Les taxons suivants de polyptychitinidés provenant du bassin de Sverdrup et d'autres bassins arctiques sont décrits et illustrés dans le présent bulletin: le genre Polyptychites, *avec* P. keyserlingi *(Neumayr et Uhlig),* P. *aff.* hapkei *nouv. esp.,* P. tschekanovskii *Pavlow,* P. *aff.* tschekanovskii *Pavlow,* Polyptychites *nouv. esp. A,* P. canadensis *Kemper et Jeletzky,* P. balkwilli *nouv. esp.,* Prodichotomites *aff.* hollwedensis *Kemper; le genre* Siberiptychites, *y compris le sous-genre* Siberiptychites s. str., *avec* S. (S.) stubendorfii *(Schmidt),* S. (S.) *nouv. esp. aff.* stubendorffi *(Schmidt),* S. (S.) fascicostatus *nouv. esp.; le sous-genre* Pseudoeuryptychites *Jeletzky 1986, avec* S. (P.) middendorffi *(Pavlow),* S. (P.) *cf. ou aff.* middendorffi *(Pavlow),* S. (P.) pavlovi *(Voronets),* S. (P.) pateraeformis *(Voronets),* S. (Pseudoeuryptychites) *nouv. esp. indét. A; et* Siberiptychites *(nouveau sous-genre)? nouv. esp. B; le genre* Astieriptychites *Bodylevsky, avec* A. obsoletus nouv. esp., A. sp. indet. A, et A? sp. indet. B*; le genre* Amundiptychites *Kemper et Jeletzky, avec* A. sverdrupi *Kemper et Jeletzky,* A. *aff.* sverdrupi *Kemper et Jeletzky,* A. thorsteinssoni *nouv. esp. et* A. fasciatus *nouv. esp. Les taxons suivants de Simbirskitinae Spath du Valanginien supérieur sont également décrits et illustrés: le genre* Ringnesiceras *Kemper et Jeletzky, y compris le sous-genre* Ringnesiceras s. str., *avec* R. (R.) amundense *Kemper et Jeletzky,* R. (R.) pseudopolyptychum *Kemper et Jeletzky,* R. (R.) tozeri *Kemper et Jeletzky et* ?R. (R.) *nouv. esp. aff.* amundense *Kemper et Jeletzky, ainsi que le sous-genre* Elleficeras *Kemper et Jeletzky, avec* R. (E.) ellefense *Kemper et Jeletzky et* R. (E.) *nouv. esp., indét.*

La génération valanginienne du bassin de la Basse-Saxe se trouvait près de la limite des royaumes fauniques arctique et mésogéen et se déplaçait aisément par voie marine d'un royaume à l'autre. Le bassin contient donc un mélange considérable d'ammonites mésogéennes caractéristiques. À la même époque, certains des polyptychitinidés caractéristiques du bassin ont migré vers le nord jusque dans les bassins arctiques de l'Eurasie et de l'Amérique du Nord. Les ammonites du Valanginien du bassin de la Basse-Saxe revêtent donc une très grande importance pour la corrélation zonale des roches valanginiennes de nature mésogéenne et des roches équivalentes subarctiques et arctiques. Les auteurs proposent un nouveau système de corrélation zonale des roches valanginiennes du bassin de Sverdrup et des roches de la Sibérie centrale, du bassin de la Basse-Saxe et de la fosse vocontienne.

INTRODUCTION AND ACKNOWLEDGMENTS

Recent stratigraphical and paleontological studies of early Lower Cretaceous rocks of the Sverdrup Basin, summarized in part by Jeletzky (1973), Kemper (1975, 1977), Jeletzky (1979) and Kemper & Jeletzky (1979), have revealed the presence of several important boreal Valanginian ammonite faunas. Some are closely allied to those of Northwest Europe, England, European Russia, European Arctic and Northern Siberia; while others are new to the science and apparently endemic.

The unexpectedly close relationships of some of the Canadian Valanginian ammonites with those of several geographically remote regions are of considerable stratigraphical, paleogeographical and paleobiotic interest. They make it possible to improve the exisiting somewhat tenuous and crude correlation of the Canadian Valanginian marine rocks with the substages and standard zones of the Valanginian stage based on the European faunas and type localities. Furthermore, they facilitate a refinement of the presently used zonal subdivision of the Valanginian marine rocks of Canada proposed by Jeletzky (1964, 1968, 1971a, b, c, 1973), Kemper (1975, 1977), Jeletzky (1979) and Kemper & Jeletzky (1979). Finally, they contribute to the elucidation of geographic relationships of various land areas of the European and North American Arctic in the Valanginian time (Kemper, 1975, p. 3, 4), particularly with reference to the conflicting interpretations recently proposed by the adherents and opponents of the global plate tectonic hypothesis.

This paper is a final report describing those representatives of the subfamilies Polyptychitinae Spath 1924 and Simbirskitinae Spath 1924 known from the Valanginian rocks of the Sverdrup Basin, District of Franklin, N.W.T. and redescribing the original material and types of closely related Polyptychitinae from the Lower Saxony Basin, Northwest Germany. The paper also evaluates the generic, taxonomic and stratigraphic relationships of the Polyptychitinae and Simbirskitinae of Arctic Canada and Northwest Germany with those of other regions of the Boreal Realm. These regions form part of many national states. Consequently, their Valanginian ammonite faunas and stratigraphy were described in many languages and the fossil collections concerned are deposited in a great number of national institutions.

In addition to the language and political difficulties encountered during this synthesis, problems have been created by the largely independent studies of Valanginian ammonite faunas in every nation involved, which have resulted in excessive taxonomic and nomenclatorial splitting. This, in turn, has obscured the degree of affinity of the faunas concerned and prompted the introduction of unnecessarily localized and complex zonal schemes (Jeletzky, 1973, p. 70). The situation is further complicated by the existence of geographically restricted faunal provinces within the Valanginian Boreal Realm. These provinces, where the localized endemic species are commonly prevalent over the interregionally occurring species, came into being because of migrations of isolated representatives of species groups which were widespread elsewhere. These migrant offshoots commonly began to evolve in their own directions after they settled in the new regions (Kemper, 1977, p. 2). The resulting morphological changes have sometimes been so substantial that the writers were unable to infer the exact generic relationships of the resulting endemic species and genera to their ancestral stocks. For example, Kemper and Jeletzky (1979) found it difficult to interpret the origin and affinities of *Astieriptychites* Bodylevsky 1960 and *Euryptychites* Pavlow 1914 in spite of the availability of well preserved and abundant comparative material from Northwest Germany. This problem was largely clarified by the more recent discovery of *Bodylevskites* (Klimova, 1978) and a study of the ontogeny of *Siberiptychites stubendorffi* (Klimova, 1981). However, other similar problems, such as the connections between *Ringnesiceras* and *Simbirskites* are left unsolved in this report, except for some tentative suggestions. In some other instances the writers were unable to interpret definitively species published by earlier workers (especially by Bogoslovsky 1902; Sokolov, 1910, 1926 and Pavlow, 1914) either because of poor illustrations or because species were based on taxonomically meaningless material (e.g. fragments of shells, juvenile specimens only). The identity of yet other species published by early workers is uncertain because their age and localities are unknown.

The principal objective of the writers' studies was a reinterpretation of previously published, nomenclatorially, taxonomically and phylogenetically important species, the description of new and stratigraphically relevant taxa and the clarification of the sequence of species. The material from Northwest Germany proved to be of decisive importance for the solution of these problems. However, only some of the most important German species are described in this paper as others were described by Kemper (1978) and Kemper & Jeletzky (1979). Furthermore, other less relevant species will be dealt with by Kemper (in preparation). His paper will include details of localities of all German Polyptychitinae species, the stratigraphic sequence of Valanginian rocks in Northwest Germany and other related data.

Because of the difficulties discussed above, the project was made a subject of team work by the authors organized by the Geological Survey of Canada and the Bundesanstalt fuer Geowissenschaften and Rohstoffe of Bundesrepublik Deutschland. The authors' specific contributions to the paper are as follows: E. Kemper is largely responsible for the taxonomic, phylogenetic and biostratigraphic re-interpretation of the Northwest Germany Polyptychitinae. However, the description and evaluation of the genus *Bodylevskites*, as well as the description, analysis and evaluation of external suture lines of all other Northwest German Polyptychitinae genera and species was researched by J.A. Jeletzky, who also participated in all other laboratory phases of the study of these forms. The same is true of E. Kemper where the genus *Bodylevskites* and the research of the suture lines of Northwest German Polyptychitinae are concerned. The authors share responsibility for all conclusions reached.

All taxonomic descriptions, phylogenetic interpretation and biostratigraphic evaluation of Canadian Polyptychitinae and Simbirskitinae are a result of joint research. However, E. Kemper is largely responsible for the treatment of *Polyptychites, Prodichotomites, Amundiptychites* and *Ringnesiceras* while J.A. Jeletzky is largely responsible for that of *Siberiptychites, Pseudoeuryptychites* and *Astieriptychites*. J.A. Jeletzky is, furthermore, responsible for the descriptions, analysis and evaluation of external suture lines of all Canadian Polyptychitinae and Simbirskitinae.

J.A. Jeletzky has written the sections dealing with methods, taxonomy and terminology employed by the authors. The English draft of the paper was arranged and, in part, translated by J.A. Jeletzky from English and German drafts of its sections written by individual authors. For technical reasons, J.A. Jeletzky has organized and edited the final manuscript and illustrations.

All conclusions about relationships of the Canadian Polyptychitinae and Simbirskitinae with their Northwest European, European Arctic and North Siberian relatives are the result of joint research by the authors who are equally responsible for these results, except where it is expressly stated otherwise. The introductory sections were also written jointly.

A veritable flood of Soviet publications dealing with the taxonomy, biostratigraphy and phylogeny of the Valanginian Polyptychitinae of North Siberia, descended on the authors a few months after the final manuscript of this paper was completed. Unfortunately, it was impossible to utilize any of them as both authors had already become heavily involved with other, urgent departmental projects. The papers included: Zakharov, V.A.; Nalniaeva, T.I.; and Shulgina, N.I.; New data about biostratigraphy of the Upper Jurassic and Lower Cretaceous deposits on the Paks Peninsula, Anabar Bay; Akademiya Nauk SSSR, Sibirskoye Otdelenie, Institut Geologii i Geofiziki, Trudy No. 528, 1983, p. 56-99, Pls. I-XXVII, 5 Text-figs., 4 Tables; Shulgina, N.I. and Burdykina, M.D.; A detailed re-study of the key sections of the Valanginian of Boyarka River — Saks Peninsula; Ministerstvo Geologii SSSR, PGO "Sevmorgeologiya". Palaeontologicheskoye obosnovaniye raschleneniya paleozoya i mesozoya arkticheskich raionov SSSR, Leningrad, 1983, p. 77-91, 4 Pls., 3 Text-figs.; Gol'bert, A.V. and Klimova, I.G.; New Valanginian ammonites of Northern Siberia; Akademiya Nauk SSSR, Sibirskoye Otdeleniye, Trudy Instituta Geologii i Geofiziki, No. 555, 1983, p. 137-154, Pls. XII-XIII, 3 Text-figs., 3 Tables; Klimova, I.G., The genus *Astieriptychites*, its ontogenesis and morphological distinctions; Akademiya Nauk SSSR, Sibirskoye Otdeleniye, Institut Geologii i Geofiziki, Trudy No. 538, 1983, p. 81-89, Pls. XVII-XVIII, 3 Text-figs.; Klimova, I.G.; The zonal complexes of lower Valanginian ammonites of northern Siberia; Ministerstvo Geologii SSSR, Sibirskii Nauchno-Issledovatel'skii Institut Geologii, Geofiziki i Mineral'nogo Ssyria. Granitsy

Krupnykh Podrazdelenii Fanerozoya Sibiri (collection of papers), Novossibirsk, 1983, p. 120-130, 1 Text-fig. to name only the most important papers.

Except for a brief summary of general biostratigraphical data and a correlation chart (Figure 62) provided at the end of the report, all pertinent stratigraphical, interregional biochronological, phylogenetical and paleobiogeographical data are provided in the description of taxa concerned. Furthermore, these descriptions include abundant cross-references to the authors' previous publications, in order to avoid a further expansion of this voluminous monograph.

This joint project was made possible by generous financial support for E. Kemper's field and laboratory work and travel in Canada by the Ministerium fuer Forschung und Technologie der Bundesrepublik Deutschland and the Geological Survey of Canada, Department of Energy, Mines and Resources. The field work in the Sverdrup Basin, N.W.T. during the summers of 1974 and 1976 was undertaken from base camps of the helicopter-equipped field party led by H. Balkwill, Institute of Sedimentary and Petroleum Geology, Calgary, whose generous co-operation is gratefully acknowledged. Dr. E. Kemper also expresses his sincere thanks to the Academy of Sciences of U.S.S.R. and the Deutsche Forschungsgemeinschaft, for the assistance which made possible his research trip to Leningrad in 1982. His study of the Siberian fossil collections in the Chernyshow Museum, Leningrad and the Institute for the Study of Geology of Arctic Seas of U.S.S.R., Leningrad was greatly facilitated by the friendly cooperation of Doctors N.I. Shulgina, J. Bogdanova and M. Burdykina. Sincere thanks are expressed herewith to these colleagues. Special thanks are due to Dr. N.I. Shulgina who provided numerous important technical data to Dr. E. Kemper. Her suggestions facilitated the correct interpretation by both authors of the genera *Siberiptychites* and *Astieriptychites*, which are so important for the biostratigraphy and paleobiogeography of the high Boreal basins of Eurasia and North America.

The authors wish to thank sincerely Dr. P.F. Rawson and Professor D.T. Donovan (London, Great Britain), Dr. J. Sornay (Paris, France) and Dr. D. Worsley (Oslo, Norway) for permission to study collections of Valanginian ammonites in their care, provision of plaster casts and/or photographs of some of these ammonites and other valuable help. Dr. P.F. Rawson has critically read the paper and made a number of valuable suggestions which improved materially the final manuscript.

Mr. H. Axmann and Mr. B. Waterstradt (Bundesanstalt fuer Geowissenschaften und Rohstoffe, Hannover) prepared numerous plaster casts of the Northwest German Polyptychitinae used by both authors and prepared some of the specimens described and figured in this paper.

Mrs. K. Vincent, formerly with the Ottawa Paleontology Section, Geological Survey of Canada, prepared some of the text-figures of this paper from drafts provided by the authors, drew some of the suture lines published in the paper and ably supervised the photographing of many of the fossils published in it. Ms. J. White, Geological Survey of Canada, photographed many of the Canadian and Northwest German ammonites figured in this paper. Mr. G. Martin, Geological Survey of Canada, prepared numerous plaster casts of the Canadian ammonites used by both authors and offered other technical help.

The following abbreviations indicate the repositories of figured and cited specimens: GSC = Collections of Geological Survey of Canada, Ottawa, Ontario, Canada; BGR = Combined collections of Niedersachsisches Landesamt fuer Bodenforschung (NLFB) and Bundesanstalt fuer Geowissenschaften und Rohstoffe (BGR), Hannover, Bundesrepublik Deutschland; GIH = Collections of Geologisches Institut der Universitaet Hamburg, Bundesrepublik Deutschland; and GIG = Collections of Geologisches Institut der Universitaet Goettingen, Bundesrepublik Deutschland.

MATERIAL

Most of the ammonites from the Sverdrup Basin described here were collected by E. Kemper, but the material is supplemented by specimens collected by Geological Survey of Canada and oil company geologists. Only a minority of the supplementary specimens lack precise stratigraphic information.

E. Kemper spent about one month each in 1974 and 1976 measuring stratigraphic sections in the Valanginian part of the Deer Bay Formation and collecting ammonites bed-by-bed (Kemper 1975, 1976, 1977). His fossil localities are shown in Figure 1. The studied sections are poor in macrofossils and thick sequences were encountered that yielded none. This precluded Kemper and Jeletzky (1979) from introducing a formal ammonite zonal subdivision for the Valanginian of the Sverdrup Basin: instead they proposed an informal nomenclature based on fossil beds. This nomenclature is largely used, with some modifications, in this final report, although it was possible to replace some of the informal names by formal regional or interregional fossil zones.

The preservation of Valanginian ammonites found in the Sverdrup Basin is mostly unsatisfactory. Many are deformed or fragmentary, and commonly only their outer whorls are satisfactorily preserved. Ontogenetic study was possible only in some exceptional instances because of a coarse calcite preservation of the inner whorls.

The Lower Saxony Basin forms part of the Northwest German Plain. Therefore, it does not offer any natural exposures of the Valanginian rocks. All ammonites used in this paper are derived from clay pits dug for brick making. Most of these pits are no longer extant. Continuous Valanginian profiles did not exist and each clay pit exposed a different level in the sequence. It was, nevertheless, possible to infer the relative positions of the individual pits within the Valanginian succession and so to recognize an approximate sequence of ammonite species (Kemper, 1978, p. 199).

As in the Sverdrup Basin, the Lower Saxony Valanginian succession includes sequences of beds that are devoid of macrofossils. However, the greatest obstacle of a study of the Northwest German material is its poor preservation. With rare exceptions, only the last whorl of these ammonites remains preserved. This peculiar type of preservation normally precludes any ontogenetic study. This is regretable, as our research has demonstrated that an investigation of ontogenetic development is very important. Therefore, problems remain unclarified.

The Northwest German fossil localities that have yielded Valanginian ammonites used in this paper are shown in Figures 2, 3, 4.

PALEONTOLOGY

Remarks on Methods, Taxonomy and Terminology

General remarks

It was originally decided to compare the newly discovered Valanginian Polyptychitinae and Simbirskitinae faunas of the Sverdrup Basin with the Polyptychitinae faunas of the Lower Saxony Basin of Northwest Germany because the latter was recognized as the principal evolutionary center of the Polyptychitinae. As already stressed by Kemper (1978, p. 186), no other Boreal region has yielded such an abundance and variety of representatives of the principal genera *Polyptychites* Pavlow 1892, *Dichotomites* Koenen 1909 and *Prodichotomites* Kemper 1971. Furthermore, it is the Lower Saxony Basin that has yielded numerous transitional forms arranging the principal species of *Polyptychites* and *Prodichotomites* into lineages as well as numerous forms connecting these two genera with one another. At the same time the basin has

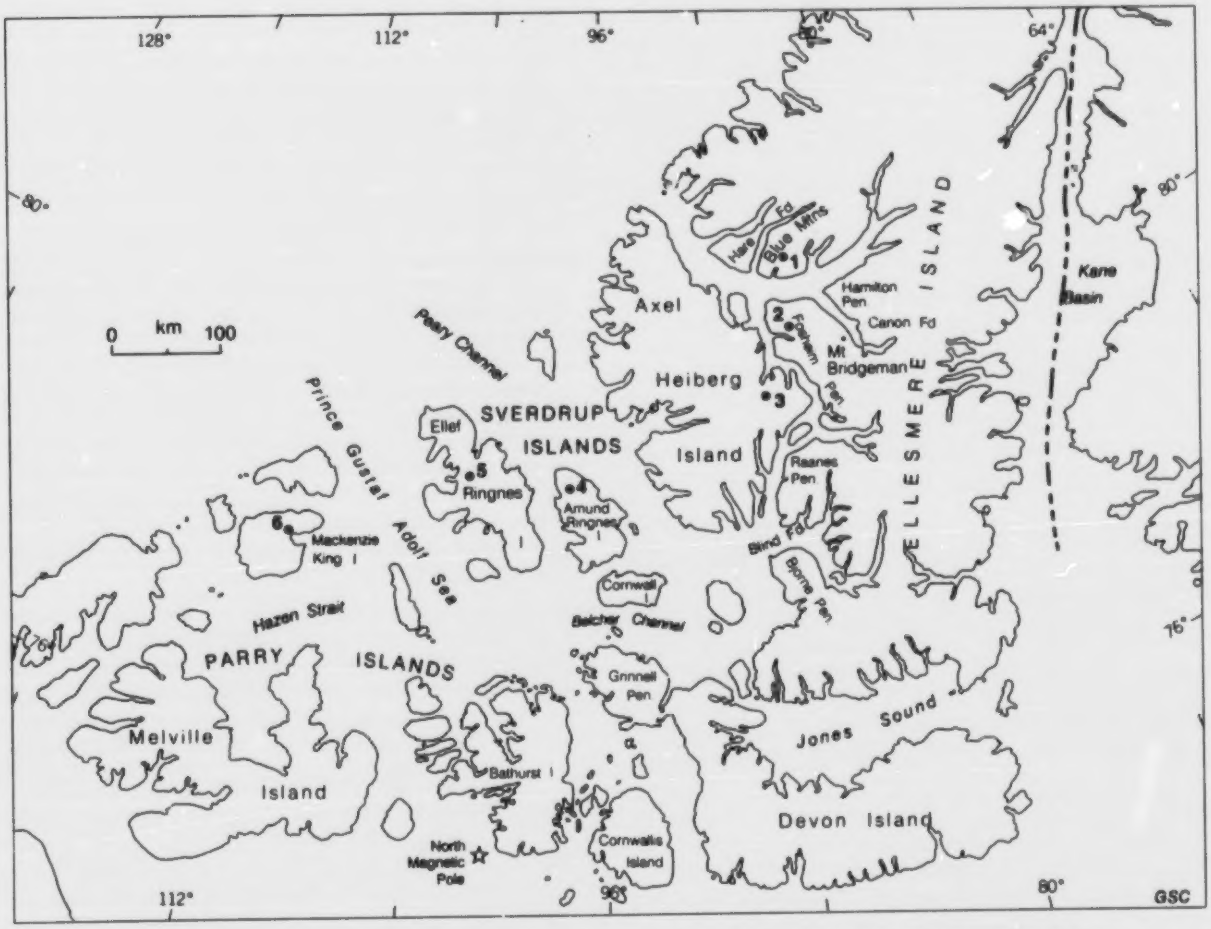

128°
112°
96°
80°
64°
80°
80°
76°
0 km 100
Peary Channel
Prince Gustaf Adolf Sea
SVERDRUP ISLANDS
Ellef
5
Ringnes
4
Amund Ringnes I
Axel Heiberg Island
Hare Fd
Blue Mtns
1
2
Fosheim Pen
3
Hamilton Pen
Canon Fd
Mt Bridgeman
ELLESMERE ISLAND
Kane Basin
Raanes Pen
Blind Fd
Bjorne Pen
6
Mackenzie King I
Hazen Strait
PARRY ISLANDS
Cornwall I
Belcher Channel
Grinnell Pen
Jones Sound
Melville Island
Bathurst I
North Magnetic Pole
Cornwallis Island
Devon Island
112°
96°
80°
GSC

Figure 1. Key map showing principal sections and localities in Sverdrup Basin that yielded Valanginian Polyptychitinae and Simbirskitinae described in this paper. 1. Blackwelder Mountains. 2. Reptile Creek near Eureka Weather Station. 3. South of Buchanan Lake. 4. North Amund Ringnes Island. 5. Ellef Ringnes Island, SW of Isachsen Weather Station. 6. Mackenzie King Island (northern part).

yielded the bulk of the oldest known and most primitive representatives of the Polyptychitinae (i.e. *Propolyptychites*, *Paratollia*, *Peregrinoceras* sensu Casey 1973 and *Bodylevskites*) that connect the subfamily with the Olcostephaninae of the northern Tethyan basins and are direct ancestors of *Polyptychites*, *Euryptychites* and *Prodichotomites*. These basal Valanginian polyptychitinds must have migrated into the Lower Saxony Basin either via the North Sea Basin or via the Central Polish Basin. Finally, the abundant polyptychitinid faunas of the Lower Saxony Basin are much better known than those of any other Boreal basin of Northwest, Central or Eastern Europe. The comprehensive publications of Neumayr and Uhlig (1881) and Koenen (1902, 1909) contain the original descriptions and excellent illustrations of the bulk of presently known European polyptychitinid taxa.

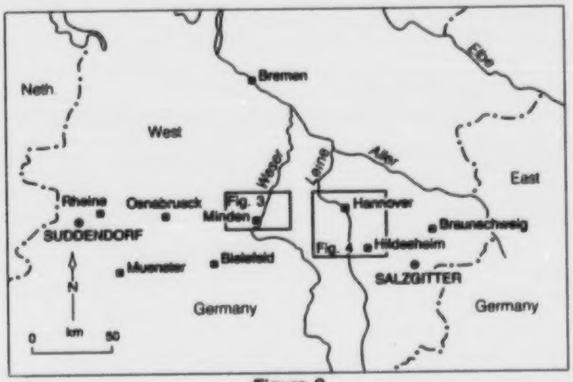

Neth
West
Bremen
Elbe
Weser
Leine
Aller
East
Rheine
Osnabrueck
Fig. 3
Minden
Hannover
Braunschweig
SUDDENDORF
Fig. 4
Hildesheim
Muenster
Bielefeld
SALZGITTER
N
Germany
Germany
0
km
50

Figure 2

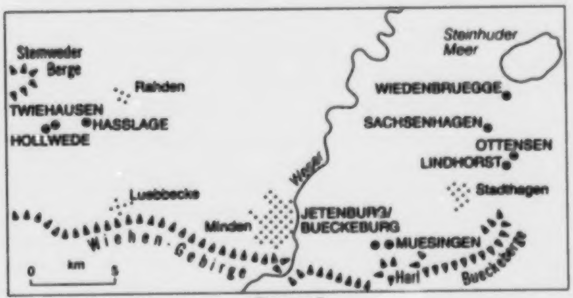

Steinhuder Meer
Stemweder Berge
Rahden
WIEDENBRUEGGE
TWIEHAUSEN
HASSLAGE
HOLLWEDE
SACHSENHAGEN
OTTENSEN
LINDHORST
Weser
Stadthagen
Luebbecke
JETENBURG/ BUECKEBURG
Minden
MUESINGEN
Wiehen-Gebirge
Harl
Bueckeberge
0
km
5

Figure 3

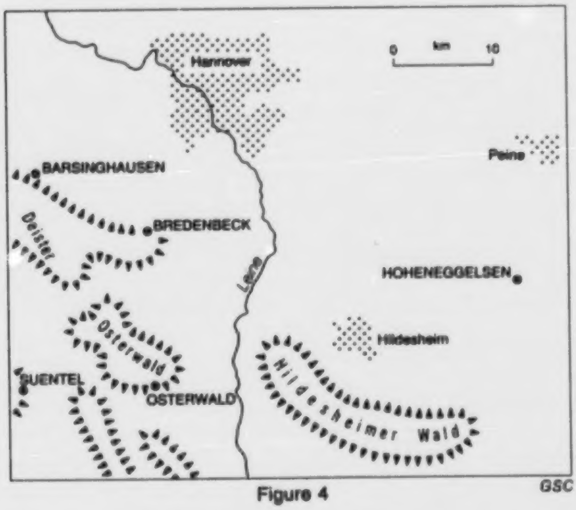

Hannover
0
km
10
Peine
BARSINGHAUSEN
Deister
BREDENBECK
Leine
HOHENEGGELSEN
Osterwald
Hildesheim
SUENTEL
OSTERWALD
Hildesheimer Wald

Figure 4

GSC

Towns and cities .... ■ ∴∴ *Principal fossils localities (clay pits)* .... ●

Figures 2-4. Key maps showing the location of principal sections and localities in the Lower Saxony Basin that have yielded Valanginian Polyptychitinae described in this paper. The location of Figures 3 and 4 are indicated on Figure 2. See Kemper (1978, p. 196-199, Figs. 4, 5) for further details.

At the onset of the project it appeared that the Lower Saxony Basin was the only significant evolutionary center of the Polyptychitinae. All other Valanginian marine basins of Europe (e.g. eastern England, Central Poland, European part of the USSR) and the Arctic (e.g. European Arctic, North Siberia and Arctic North America) appeared to have been populated largely or entirely by depauperated faunas of polyptychitinid migrants from the Lower Saxony Basin. However, it soon became evident (Kemper, 1977, p. 3; Kemper and Jeletzky, 1979) that the actual situation was much more complex. The idea that the polyptychitinid stocks of all the marine basins mentioned above were derivatives of Lower Saxony lineages was found to be essentially correct. However, it became obvious that the migrants experienced a considerable endemic evolution in each basin and produced a number of local polyptychitinid lineages, including taxa of generic and even subfamilial (e.g. Simbirskitinae) rank. This situation is exemplified by the development of *Siberiptychites* and *Astieriptychites* lineages from the migrant *Bodylevskites* stock in central North Siberia and by the development of *Ringnesiceras* lineage in the Sverdrup Basin from some late *Polyptychites* stock. Polyptychitinae conspecific and even congeneric with those of the Lower Saxony Basin were found to be relatively rare in the high Boreal (or Arctic) Valanginian basins. Furthermore, they were found to be confined to several restricted stratigraphical levels (Kemper, 1977, p. 3, Fig. 2; Kemper and Jeletzky, 1979) that appear to represent the times of widespread transgressions that facilitated the "escapes" of the Lower Saxony polyptychitinids into the high Arctic basins. These inferred migrations and endemic evolutionary developments are summarized in Figure 11.

The writers adhere to a moderately conservative concept of all taxa used. At the generic and higher levels, their approach approximates the "middle of the road" taxonomic and nomenclatorial procedures adopted in the Ammonoidea volume of the Treatise on Invertebrate Paleontology (Arkell et al., 1957) and the Ammonoidea-Endocochlia volume of the Soviet Osnovy Paleontologii (Luppov and Drustchits, Editors, 1958; see Khimiashvili et al., 1958). The more radical taxonomic and nomenclatorial approach practiced by a great many contemporary ammonitologists studying olcostephanid and craspeditid ammonites (e.g. Casey, 1973; Shulgina, 1965, 1968; Saks and Shulgina, 1969; Sazonova, 1971, 1977; Saks et al., 1972, Bodylevsky, 1967) is not accepted as it results in excessive splitting and grossly overcomplicated, entirely artificial paleontological systematics at the specific and higher levels. This appears to hinder rather than further the understanding of the evolutionary development and paleobiotic radiation of ammonites (or for that matter of any other group of fossils) and hence their biochronological utilization. Most of the reasons underlying the decided opposition of the writers to such an excessive splitting of ammonite taxa have been published already (e.g. Jeletzky, 1950, 1955, 1965a, p. 3-15) and do not need to be repeated here. However, they will be commented on more specifically below in connection with the description of the individual polyptychitinid and simbirskitinid taxa.

Like classifications of all other groups of fossil organisms, this attempt to re-classify the presently known Valanginian representatives of Polyptychitinae and Simbirskitinae is an entirely empirical undertaking. It is based on the study of the behaviour of all observable morphological characters. The degree of stability (or lack thereof) of these characters in time and space was used to work out their taxonomic hierarchy. The greater the degree of stability the higher the rank that was assigned to the morphological characters concerned. Conversely, the greater the degree of variability within the shortest intervals of geological time and the smallest, most intimately related groups of fossils, the lesser the taxonomic rank that was allotted to them.

The second, closely related taxonomic criterion used is the presence or absence of intergradation of morphological characters within form groups that occur in the same bed(s) within either a well defined basin or one of its lithofacies. The existence (or the likelihood) of morphological intergradation among such geologically contemporary, simpatric forms was, as a rule, interpreted to mean that they are either variants of a polytypic species or its simpatric subspecies, regardless of how marked their morphological extremes may be. *Polyptychites keyserlingi* s. lato provides an excellent example of such a polytypic species. The presence of well documented or probable gaps between the morphological extremes of such form groups was, in contrast, interpreted to indicate that they are independent co-existing species.

Even the slightest morphological distinctions were judged to be of either a specific or even higher rank whenever they were found to be constant and the fossils exhibiting them were confined to different stratigraphic levels. In all such instances, the morphological intergradation of the forms concerned at intermediate stratigraphic levels was interpreted as an indication of their direct ancestor-descendant relationships. Most of the Polyptychitinae and Simbirskitinae lineages discussed below and recognized as valid are based on such observations. Whenever such morphological intergradation was observed, the successive members of resulting evolutionary lineages had to be purely arbitrarily delimited. The Northwest German representatives of *Polyptychites* and *Prodichotomites* described below provide a number of examples of such morphological intergradation on the specific level. Furthermore, these two genera were found to be connected by a host of morphologically transitional forms that can be only arbitrarily assigned to one of them. The recent study of the Northwest German representatives of *Dichotomites* s. str. (Kemper, 1978) has also demonstrated morphological intergradation of a number of its species.

Slight morphological distinctions of obviously closely allied, geologically contemporary to near contemporary forms were treated as very significant taxonomically whenever such forms were found to be confined to geographically remote regions forming part of different paleobiogeographical provinces or subprovinces within the Boreal Realm. It was reasoned (e.g. Kemper, 1977, p. 3, 4, Fig. 2 and in this paper) that such paleogeographic separation indicates that these slightly different forms are vicarious species that "escaped" from their original evolutionary center and began to evolve independently from their closest allies in their new habitat areas. Most such vicarious species were found to be the rootstocks of endemic groups of forms that had to be treated as independent subgenera or genera. That happened, for example, with the North Siberian *Bodylevskites* species that presumably migrated there from Northwest Europe and evolved into a group of distinctive North Siberian and Arctic Canadian polyptychitinid genera described below (e.g. *Sibiriptychites*, *Pseudoeuryptychites*, *Astieriptychites*, *Amundiptychites*). Another somewhat less definitively documented example is provided by *Polyptychites michalskii* that migrated to Central Russian and North Siberian basins and evolved either there or somewhere else in the Boreal Realm into the paleosimbirskitid genus *Ringnesiceras*. Other instances are known, however, when such migrants either only produced new species of the same genus or even did not evolve beyond a vicarious subspecies. For example, *Polyptychites* ex gr. *hapkei* n. sp. that migrated into the Valanginian basins of North Siberian and Arctic Canada apparently only produced there the closely related *P. tschekanovskii*. The rare North Siberian and Sverdrup Basin representatives of *Prodichotomites* aff. *P. hollwedensis* Kemper apparently did not give rise to any endemic lineages.

The later phases of the writers' research had demonstrated that the regional lineages of Polyptychitinae and Simbirskitinae that arose in Northern Siberia and Arctic Canada tended to evolve either parallel with or convergent to the Polyptychitinae lineages of the Lower Saxony Basin. This resulted in many of their advanced representatives being nearly identical homoeomorphs of the contemporary Lower Saxony forms. The recognition of this fact necessitated the closest possible scrutiny of all morphological features of the Sverdrup Basin ammonites that appeared earlier to be congeneric or even conspecific with the European and/or North Siberian forms (e.g. Jeletzky, 1964; 1973; Kemper, 1975, 1977). This scrutiny had revealed that a number of these Sverdrup Basin forms are actually only homeomorphs of their European and North Siberian analogues (*see* Kemper and Jeletzky, 1979 and below).

Comparative taxonomic value of morphological features

Suture line.

The previously discussed mode of preservation of the Northwest German and Canadian material studied has made it impossible, as a rule, to study the suture lines of the early and intermediate whorls. This preservation also precluded the study of the internal parts of the suture lines. Consequently, only the external suture lines of adult ultimate and adult penultimate whorls were consistently available for study. Therefore, it was impossible to study the ontogenetic development of the complete suture lines of our material in the way that Schindewolf (1966), Klimova (1978, 1981) and Alekseev (1982) did for some of the Eurasian polyptychitinids. Furthermore, it was impossible to apply the genetic terminology of complete sutures used by these workers to our material. Instead, the writers were forced to use the purely morphological terminology of the suture lines originally applied to the external suture lines of Olcostephanidae by Pavlow (in Pavlow and Lamplugh, 1892) and used widely ever since in the Russian literature (including the Osnovy Paleontologii; see Khimiashvili et al., 1958, p. 16, 93-95, Figs. 77, 78). This so called Russian system (see Jeletzky, 1965b, p. 2) is most convenient for the olcostephanid and craspeditid perisphinctids because they exhibit a sublinear arrangement of most or all elements of their external sutures coupled with the presence of two orders of lobes. Their large, first order lobes are separated by (mostly wide) saddles, the tops of which are dissected by considerably smaller, ordinarily easily distinguishable lobules. The two first order lobes situated on the flank next to the ventral lobe (designated V) are designated the first (L1) and the second (L2) lateral lobes (Figure 5). All other first order lobes situated between the second lateral lobe and the umbilical seam are termed the auxiliary lobes and designated Al to An, depending on their number. Their number is not known to exceed five in the Olcostephanidae. There are, for example, five auxiliary lobes designated A1 to A5 inclusive in the external suture line of *Dichotomites tardescissus* Koenen 1902 reproduced in Figure 5. The much smaller, second order lobes subdividing the tops of saddles are termed lobules. They are not numbered in any way. The saddle separating the ventral lobe from the first lateral lobe is termed the first lateral saddle (S1) while all other first order saddles visible on the flank and umbilical wall are numbered successively second, third, etc. lateral saddles. For example, in the suture line shown in Figure 5 there are eight of them designated S1 to S8 inclusive.

The term **adult external suture line** is restricted to those sutures of advanced to final adult whorls that exhibit the maximum number of well developed auxiliary lobes. Such sutures are retained to the oral end of adult phragmocone and are characteristic of the species and genera concerned. In the material studied here this type of external suture line is mostly restricted to the adult penultimate whorl and the immediately preceding two to several whorls. The adult external suture line may appear earlier in some of the Polyptychitinae species studied (e.g. in *Siberiptychites stubendorffi*; see Figure 52 or *S.* (*Pseudoeuryptychites*) spp., see p.176). However, it may be restricted to only two oralmost whorls of the adult phragmocone in other closely related taxa (e.g. *Siberiptychites* (*Pseudoeuryptychites*) *middendorffi*; see p.170).

The adult external suture line extends onto the initial part of the last whorl in those species where the living chamber is less than one whorl long. In spite of a characteristic simplification of the last few sutures, they retain the maximum number of auxiliary lobes attained on the earlier part of the penultimate whorl.

The external suture lines of earlier whorls are characterized either by a reduced number of auxiliary lobes or by the ill-defined character of the adumbilicalmost part of the sutures (as defined by Jeletzky, 1979, p. 4, Footnote) that does not permit differentiation between the

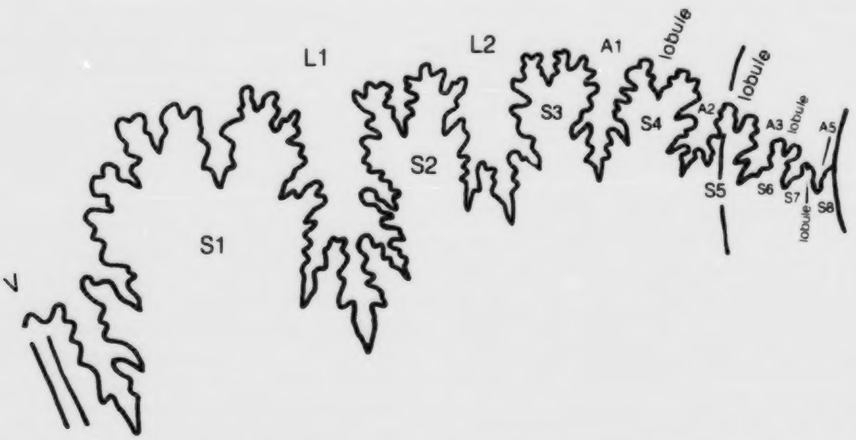


Figure 5. Adult external suture line of *Dichotomites tardescissus* Koenen, x2, wh = 45 mm. BGR, kv 376, Hannover. Varlheide-Sued, Upper Valanginian.

lobules and the true auxiliary lobes. These, usually markedly retractive, parts of the polyptychitinid suture line (e.g. Klimova, 1978, Figures 3-6; 1981, Figure 3) closely resemble the auxiliary parts of adult external suture lines of *Spiticeras* (compare Arkell et al., 1957, p. K346, Fig. 454-1a; Khimiashvili et al., 1958, p. 95, Fig. 78a) and other Olcostephaninae and are interpreted as their recapitulation. A taxonomic use of these juvenile external suture lines alone can be misleading and is not recommended. However, they may be useful if their morphological differences from the adult external suture lines of the same taxa are known and only the equivalent suture lines of these taxa are compared.

The taxonomic use of adult external suture lines at the specific and generic levels is not always easy. The underdeveloped character of juvenile suture lines may sometimes persist almost or even right up to the oral end of an adult phragmocone as illustrated by Figures 14a, 19, 25a-25c, 33a, 34a, 47b, 61c. Some of these aberrant adult sutures are characterized by the *Spiticeras*-like appearance of their adumbilicalmost parts (e.g. Figures 14a, 16c, 33a, 41b). In this case it may be impossible to reach any definite conclusion about the true nature of these adumbilicalmost sutural elements and hence to count the number of their auxiliary lobes. In other aberrant adult sutures several adjacent adumbilicalmost lobe-like elements are subequal to equal in size and have an otherwise similar appearance (Figure 61c). In this case it may only be possible to select the true auxiliary lobes using their positions in relation to the last (i.e. adumbilicalmost) clearly recognizable auxiliary lobe. This procedure is based on the observation that, as a rule, only one lobule occurs between the adjacent auxiliary lobes in the two to four adumbilicalmost lateral saddles of Polyptychitinae. The third type of aberrant adult suture line is characterized by pronouncedly narrowed adumbilicalmost saddles and an almost complete to complete absence of recognizable lobules within them (see Figures 5, 28a, 28b, 32b). This aberration is likewise apt to preclude the definitive recognition of one or two adumbilicalmost auxiliary lobes. However, it may be possible to infer the true nature of these auxiliaries because of the presence of incipient lobules in the middle of the strongly narrowed adumbilicalmost saddles. The suture of *Dichotomites tardescissus* shown in Figure 5 was decifered using this method. The method can also be applied to the suture line of *D. triptychoides* figured by Kemper (1978, Fig. 6) and to the sutures of *Polyptychites multicostatus* figured below (Figures 28a, 28b). The fourth, and the last known, aberration consists of an irregularly shaped and spacially displaced character of the adumbilicalmost part of the adult external suture line commented upon below in the description of *Hollwediceras sphaericus* and *Polyptychites tschekanovskii* (see p.88, 89, 122, Figures 34a, 47b).

The first three aberrations appear to be caused by a retarded ontogenetic development of the external suture line in some representatives of the species concerned that reflects the generally recapitulative mode of its development from the juvenile external suture lines. It is well established that the lateral part of the external suture line develops its adult morphological features and becomes stabilized before its other parts. The same happens then successively with the outermost umbilical, intermediate umbilical and, finally, innermost umbilical parts of the external suture line. Consequently, additional elements of the adumbilicalmost part of the external suture line continue to arise and then to change their appearance during those late stages of ontogeny when its lateral and outermost umbilical elements have already stabilized. These ontogenetic stages being close to the adult state, a sporadic occurrence of aberrant features in the latter is quite understandable.

The fourth type of morphological aberration appears to be pathologically caused. Therefore, it does not appear to have any ontogenetic significance.

The only way to cope with taxonomic uncertainties caused by the aberrations is to prepare and to study several adult external suture lines in several representatives of the polyptychitinid and simbirskitinid species concerned in order to recognize the normal appearance of their adumbilicalmost segments and to reject the abnormal ones.

As already mentioned, the use of a purely morphological sutural nomenclature and the taxonomical utilization of the adult external suture line was dictated by the unfavorable preservation of the material studied. However, this approach has several practical advantages in comparison with the ontogenetic method of study of the complete suture line.

It is well established (e.g. Mikhailova, 1982) that the taxonomically higher ranking morphological features of an ammonite suture line tend, generally speaking (i.e. exclusive of the so called neothenic or prophetic ontogenetic mode), to arise earlier than the taxonomically lower ranking features. Furthermore, the sequential appearance of all sutural morphological features usually occurs in order of their decreasing taxonomic grade. This gradual development of the suture line ends in its becoming morphologically stabilized in all its essential features in all ammonite species. This applies to the number of its lobes and saddles, their shape and proportions, the orientation of the suture line and the degree of denticulation of all its elements. This stabilized, or adult suture line is then retained essentially unchanged to the oral end of the adult phragmocone, except for a marked simplification and approximation of its last few examples. It is this mode of ontogeny that makes the adult external suture line (and also the complete adult suture) particularly useful for the differentiation of species and genera and their grouping into subfamilies. The earlier sutures, previously termed juvenile external suture lines, are, in contrast, particularly suitable for the differentiation of the higher taxa, especially suprafamilial ones. The same is true of the complete juvenile suture lines studied by Schindewolf (1966), Klimova (1978, 1981) and Alekseev (1982). These suture lines still lack the morphological details diagnostic of the lower taxa.

Another practical advantage of the taxonomic utilization of adult external suture lines alone is that it avoids the destruction of valuable ammonite shells which is inevitable in all studies concerned with the ontogenetic development of complete suture lines. This destruction of the best specimens available is only admissible in special studies aimed at the unravelling of phylogenetic relationships of higher taxa and using specially collected, abundant material of all species concerned. This seldom happens in practice. Furthermore, the exclusive taxonomic use of adult external suture lines avoids a great investment of time and labour. Ontogenetic studies are not really necessary in studies such as ours concerned with the description and taxonomic arrangement of lower taxa.

Because of the above considerations, the writers do not believe that the exclusive study of adult external suture lines is just an emergency method subject to a complete replacement by an ontogenetic study of complete suture lines as soon as an appropriate number of sufficiently well preserved shells of the forms concerned would become available. In their opinion, the exclusive study of adult external suture lines is quite capable either to contribute to or to produce valid taxonomies and phylogenies of lower ammonite taxa, including subfamilies and even families, that can be used biostratigraphically and paleozoogeographically without any aid of the ontogenetic studies of complete suture lines. The latter are only needed ultimately for valid phylogenetic arrangements of higher ammonite taxa beginning with their superfamilies and suborders. It is unreasonable to expect all ammonite specialists, who commonly are primarily interested in the study and taxonomic arrangement of the lower taxa and their biostratigraphic use, to become involved in the time consuming and material destructive ontogenetic studies of complete suture lines. It is felt strongly that because of the above discussed practical advantages of the study of adult external suture lines alone these two methods are destined to coexist side by side so long as the ammonites will be studied and used biostratigraphically.

In the case of phylogenetic relationships of the Polyptychitinae, the study of the ontogeny of their complete suture lines seems to be of little practical value. As demonstrated below, the study of their adult external suture lines and their comparison with those of the Craspeditidae does not answer the long disputed question of the phylogenetic relationships of these two taxa. However, a recent special study of the ontogenetic development of complete suture lines of Polyptychitinae and Craspeditidae (Alekseev 1982) failed to answer it either, since they show a very similar development (Alekseev 1982, p. 128). As Alekseev points out, this could indicate derivation of the Polyptychitinae from the Craspeditidae. However, the geological history of the polyptychitinid suture line analyzed by Jeletzky (1979, p. 4, Figure 1) and discussed comprehensively below (see p.12) decidedly contradicts any such suggestion.

The adult external suture line differentiates representatives of the Polyptychitinae from those of the apparently directly ancestral subfamily Spiticeratinae Spath 1924. The latter subfamily is characterized by a much stronger suspensive, but little differentiated auxiliary part of the suture line (see Arkell et al., 1957, p. L346, Fig. 454-1a; Khimiashvili et al., 1958, p. 95, Fig. 78a) closely resembling that of the Late Jurassic Perisphinctidae (compare Khimiashvili et al., 1958, p. 85-90, Figs. 70-73). However, the adult external suture line does not seem to permit representatives of the Polyptychitinae to be distinguished from those of the directly descendant Simbirskitinae for reasons presented later (see also Khimiashvili et al., 1958, p. 94, Fig. 77).

The adult external suture line of the subfamily Olcostephaninae Haug 1908 differs from that of the Polyptychitinae in the same morphological features as that of the Spiticeratinae (compare Khimiashvili et al., 1958, p. 95, Figs. 78b, 78v). The relatively more primitive, pronouncedly Perisphinctidae-like character of the olcostephanid suture as compared with that of the approximately contemporary Polyptychitinae, is ascribed tentatively to the circumstance that the Olcostephaninae are direct, relatively little changed descendants of the Spiticeratinae. They have largely occupied the same low latitude Tethyan climatic belt as the Spiticeratinae and only occasionally invaded adjacent parts of the relatively cooler Boreal climatic belt. The Polyptychitinae represent, in contrast, a specialized offshoot of the Spiticeratinae (see Figure 11). They migrated to the Boreal climatic belt before the beginning of the Valanginian (probably in the late Berriasian; see p. 18) and rapidly adapted to their new habitat. This adaptation appears to be expressed in the modification of the suture line and in morphological changes of other features (see below) convergent to those of the family Craspeditidae.

Jeletzky's (1965b, p. 2) conclusion that the adult external suture line of *Polyptychites* has two or, more rarely, three auxiliary lobes remains valid for all presently known representatives of that genus. However, Jeletzky's (1979, p. 4) conclusion that: "None of the elements of the external suture line, judged to be taxonomically valuable at the subfamily level, seems to change materially within the subfamily Polyptychitinae (Text-fig. 1). These features (see Jeletzky, 1965b, p. 2, 3 for further details) are considered accordingly the most reliable means for its recognition." is invalidated by the subsequent research of the writers. Even the Northwest and Central European representatives of Polyptychitinae, such as the representatives of the late Valanginian genera *Dichotomites* Koenen 1909 and *Prodichotomites* Kemper 1971, were found to possess commonly (but not invariably) a suture including four to five auxiliary lobes (e.g. Kemper, 1978, Text-fig. 6; this paper, Figures 5, 46a, 46b). This suture line was termed the **advanced polyptychitinid suture line** by Kemper and Jeletzky (1979, p. 3, footnote). Furthermore, similar adult external suture lines were found to occur in the late early and late Valanginian relatives of *Polyptychites* endemic to the North Siberian basins and the Sverdrup Basin (e.g. *Amundiptychites* and some representatives of *Siberiptychites* and *Ringnesiceras*; see Kemper and Jeletzky, 1979, p. 3, Fig. 3 and this paper, Figures 55a, 58d, 59a-59c, 61d). This advanced polyptychitinid suture line remains distinguishable from that of the contemporary craspeditids (e.g. *Homolsomites* ex gr. *quatsinoensis-bojarkensis*; see Shulgina, 1965, Pl. II, fig. 1; Pl. III, fig. 1a and Jeletzky, 1979, Fig. 1U) in the considerably broader and stubbier, less denticulated lobes and saddles and in the considerably less ascendant course of its lateral part. Furthermore, its auxiliary part is orientated either subtransversely or markedly suspensively, unlike that of the contemporary *Homolsomites*. However, this polyptychitinid suture line cannot be reliably distinguished from the less elaborate and less ascendant external suture lines of older Valanginian and Berriasian Craspeditidae, such as *Temnoptychites* and *Tollia* (compare Jeletzky, 1979, Text-figs. 1N, 1P, 1R, 1S, 1T and 1V).

The above data make it difficult and sometimes impossible to use the external suture line of Polyptychitinae as a leading diagnostic feature that differentiates this subfamily from all known representatives of the Craspeditidae. However, they do not invalidate Jeletzky's (1979, p. 3, 4, 6) conclusion that the subfamily Polyptychitinae is an offshoot of the Berriasian Olcostephanidae (i.e. Spiticeratinae). As he pointed out, the morphologically most primitive adult external suture lines of Polyptychitinae (e.g. those of *Bodylevskites* and *Paratollia*; see p.18, 24, Figures 12, 13a), that are characterized by a suspensive orientation of their auxiliary lobes and the presence of only two auxiliaries, appear in the early early (but probably not the earliest) Valanginian. All of the contemporary and earlier Cretaceous (i.e. Berriasian) adult external suture lines of Craspeditidae are evolutionarily much more advanced. They are distinctly to pronouncedly ascendant through most or all of their extent and possess four to five auxiliary lobes (see Jeletzky, 1979, p. 4-6, Text-figure 1). Even the uppermost Jurassic (i.e. late Volgian or late Tithonian) ancestors of these Craspeditidae have adult external suture lines that are sublinear to linear throughout their extent, distinctly to strongly ascendant and have three to four auxiliary lobes (e.g. *Praetollia* and *Craspedities* (*Taimyroceras*); see Jeletzky, 1973; 1966). Finally, these craspeditid sutures merge imperceptibly into the typical dorsoplanitid sutures of the latest Portlandian Dorsoplanitidae via those of the English *Swinnertonia*. These data indicate clearly that the earliest known most primitive Polyptychitinae must be offsprings of some late Berriasian Olcostephanidae (i.e. Spiticeratinae) that have closely similar adult external suture lines.

It is equally impossible to derive any of the more advanced and younger (i.e. late Valanginian) adult external suture lines of the Polyptychitinae from the morphologically similar adult external suture lines of the Berriasian and early Valanginian Craspeditidae. As already documented by Kemper (1978, p. 190-196) and confirmed by the subsequent research of the writers, the Northwest German *Dichotomites* and *Prodichotomites* are direct offsprings of the latest early to earliest late Valanginian *Polyptychites*. *Prodichotomites* evolved from the late early Valanginian *Polyptychites* ex *gr. multicostatus-saxonicus-orbitatus* (Figure 11) that is characterized by a more advanced *Polyptychites* s. str. suture line with only three auxiliary lobes. These advanced *Polyptychites* s. str. occur in beds that immediately underlie those containing the earliest and most *Polyptychites*-like representatives of *Prodichotomites* ex gr. *hollwedensis-polytomus* and are connected with them by numerous morphologically transitional forms. Though *Dichotomites* s. str. is not an offspring of *Prodichotomites* according to the latest data available (see p. 90 and Figure 11), it is a descendant of the earliest late Valanginian *Polyptychites* ex gr. *polyptychus*. The North Siberian *Siberiptychites*, *Pseudoeuryptychites* and *Astieriptychites* are certainly direct descendants of the early early Valanginian *Bodylevskites* (see p.20, 21 and Figure 11) whilst *Amundiptychites* is a derivative of the late early Valanginian *Astieriptychites* (Kemper and Jeletzky, 1979, p. 4, Fig. 8 and below). In contrast, the late Valanginian *Homolsomites* merges into the early Valanginan *Tollia* and through the latter into the Berriasian *Surites*. The latter genus merges, in turn, into the previously discussed early Tithonian (=late early Volgian) dorsoplanitids (see Jeletzky, 1979, p. 3-7, Figure 1).

Sculpture of the shell.

As pointed out by Kemper (1978, p. 188), the terminology of the extremely complex and variable sculpture of Polyptychitinae was in a state of confusion at the time of his study. Kemper's (1978, p. 188-190, Figs. 1, 2) attempt to remedy the situation is considered to be generally valid as far as it goes. The following comments expand and partly modify his suggestions and fill in some gaps in his nomenclature. All German terms used by Kemper (l. cit.) are either anglicized or replaced by already existing English equivalents.

The **primary ribs** (= Primaerrippen) are thin to fairly thin, subradial to slightly forwardly concave (i.e. comma-like) elevations that arise somewhere on the umbilical wall, extend across it and the umbilical shoulder and end somewhere (mostly low) on the shell's flank by splitting into two or more secondary ribs. The thickness and height of the primary ribs remain subequal throughout their extent in the Polyptychitinae. However, their mid-lateral ends become markedly elevated or distinctly tuberculated in the late Valanginian Simbirskitinae (see below for further details).

The adumbilical parts of primary ribs are almost invariably transformed into comma-shaped, strongly elevated and thickened, transversely elongated structures termed **umbilical bullae** (= Zirkum-umbilikal Erhoehungen) on the intermediate and/or adult whorls of Polyptychitinae. Only in some of the earliest known representatives are primary ribs retained to the oral end of their adult shells (e.g. in *Bodylevskites*, *Paratollia*, *Propolyptychites* and the most primitive *Polyptychites* species, such as *P. michalskii* and *P. oerlinghusanus*). Whenever the primaries become transformed into adumbilical bullae, they become shortened (Figure 6). This results in a marked lowering of their branching points, which tend to become coincident with the tops of their bullae. The innermost parts of these bullate primaries situated on the inner part of the umbilical wall usually retain their thin and only slightly elevated proportions.

The **secondary ribs** (= Sekundaerrippen) branching off the tops of either primary ribs or the umbilical bullae (Figures 6, 7) are usually slightly to considerably thinner than their primaries. They may extend across the middle or the middle and upper part of the flank and onto the shell's venter without any further subdivision and there join the secondary ribs of the opposite flank (e.g. in the simple dichotomous mode of bundling). Alternatively, and more commonly, some or all of the secondary ribs may split up into equally fine or yet finer **tertiary ribs** (= Tertiaerrippen) higher on the flank (Figure 6). In that case it is the secondary and tertiary ribs combined that extend onto the shell's venter. In some exceptional instances the tertiary ribs may also subdivide on the upper flank giving rise to the **quaternary ribs** (e.g. Figure 6).

The term **supplementary ribs** is proposed herein for the secondary, tertiary, intercalated and, whenever present, quaternary ribs combined.

The characteristically irregular mode of joining of supplementary ribs of the two flanks on the venter was already stressed by Kemper (1978, p. 190, Fig. 2). It is illustrated by Figure 8. It must be pointed out in this connection that the supplementary ribs of Polyptychitinae are not known to either weaken or become interrupted on the venter. As already pointed out by Jeletzky (1979, p. 7), this feature facilitates a reliable differentiation of Polyptychitinae species from some of the nearly completely homoeomorphic craspeditid species.

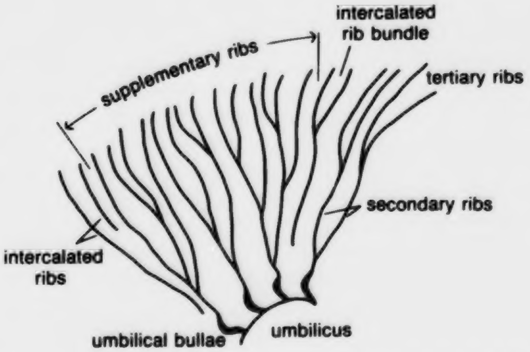


Figure 6. Schematical reproduction of types of sculpture of an adult polyptychitinid on the example of *Prodichotomites polytomus* (Koenen, 1902), X 1.

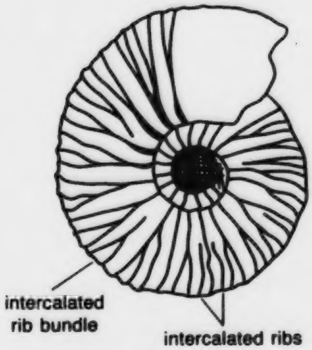


Figure 7. Schematical reproduction of types of sculpture of a juvenile polyptychitinid on the example of *Polyptychites pavlowi* Koenen 1909 reproduced in Pl. 5, fig. 3c, x 1. The first feeble bullae appear on the oralmost part of the whorl. The rest is ornamented exclusively by primary ribs that form several types of bundles.

Sigmoidal to approximately straight, round bottomed constrictions, that tend to follow the course of adjacent primary and supplementary ribs on the flank and venter, occur in some groups of Polyptychitinae while being apparently absent in the Valanginian Simbirskitinae studied. These constrictions are, as a rule, either restricted to the internal mould or much more strongly expressed there in comparison with the outer surface of the shell. These constrictions are, as a rule, restricted to the high Boreal evolutionary development of Polyptychitinae (see p. 21 below for further details) while being constantly absent in their Northwest and Central European evolutionary development (i.e. in the genera *Paratollia*, *Propolyptychites*, *Neocraspedites*, *Euryptychites* s. str., *Hollwediceras* n. gen., *Prodichotomites* and *Dichotomites* s. str.). Only the European representatives (i.e. *Bodylevskites pumilio*) of the rootstock of these two evolutionary developments differ in the possession of the constrictions.

Intercalated secondary ribs (= Schaltrippen of Kemper, 1978, p. 189, Fig. 1) beginning at variable heights on the flank and **intercalated rib bundles** consisting of secondary and tertiary ribs occur commonly between regularly formed rib bundles of any type (Figures 6, 7). These intercalated ribs and bundles are not attached either to the primary or the supplementary ribs of adjacent bundles.

Kemper's (1978, p. 188-190, Fig. 1) classification of rib bundles of Polyptychitinae is considered to be generally valid. It is used herein with some modifications and additions (Figure 9).

The "bimonotom" bundles of the tomoid class of Kemper (l. cit.) are deemed to be superfluous and misplaced. They are synonymized with the "trivirgatitpartitious" bundles of the virgatitpartitous class (Figure 9) as they appear but a slight variation of the latter. In the tomoid class this type of bundle is replaced by *monodichotomous* (or simple dichotomous) type of rib bundles that was not included in the original classification. Furthermore the *fasciculate* (= fasciat of Kemper, 1978,

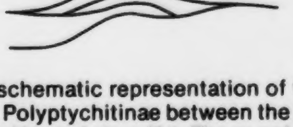


Figure 8. A schematic representation of the course of rib bundles in Polyptychitinae between the opposed ventral shoulders. Ventral view, X 1. The supplementary ribs on the venter do not join their counterparts on the other flank but are always divided between those of adjacent rib bundles (from Kemper, 1978, p. 190, Fig. 2).

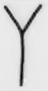
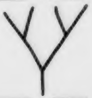
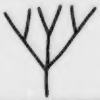
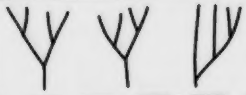
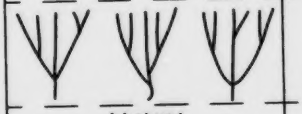
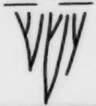
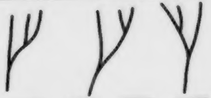
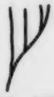
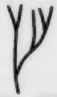
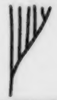
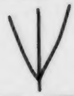
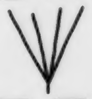
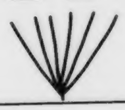
Graphic representation of bundles	Number of supplementary ribs		Principal sculptural groupings
	Number of secondary ribs	Number of tertiary quaternary and intercalated ribs	
	mono	dichotomous	Tomoid sculpture Furcation points situated at the same height. Ribbing habit regular
	bi	dichotomous	
	tri	dichotomous	
	oligo	ptychous (four to five ribs)	Ptychoid sculpture Furcation points situated at different heights. Ribbing habit irregular
	poly	ptychous (five to six ribs)	
	hetero	ptychous (very dense sculpture with many intercalated ribs)	
	tri	virgatitpartitous (=bimonotom of KEMPER, 1978)	Virgatitoid sculpture Furcation points situated at different heights but the supplementary ribs branch regularly in adoral direction
	quadri	virgatitpartitous	
	sub	virgatitpartitous	
	poly	virgatitpartitous	
	tri	fasciculate	Fasciculate sculpture All secondary ribs branch at the same height. Tertiary ribs absent
	quadri	fasciculate	
	poly	fasciculate	

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Figure 9. Sculptural types of rib bundling of Olcostephanidae. Modified from Kemper (1978, Figure 1). See text for further details.

Fig. 1) bundles are subdivided into *trifasciculate, quadrifasciculate* and *polyfasciculate* (Figure 9).

It should be stressed that the use adopted here of the "*polyptychous bundle*" for bundles consisting of five to six variably arranged secondary and tertiary ribs (Figure 9) conflicts with the currently prevalent use of that term in the Soviet literature. There the polyptychous bundle is used for the trivirgatitpartitous bundle of our classification. This usage, which apparently originated with Pavlow (1914, p. 19, 20, 24, 25, etc.), is inadmissible. The new specific name *Ammonites polyptychus* was erected to denote that this ammonite is characterized by complex, repeatedly bifurcating rib bundles consisting of five or more secondary and tertiary ribs (Keyserling, 1846, p. 327, Pl. 21, fig. 1). Furthermore, the subgenus *Polyptychites* Pavlow 1892 was expressly proposed for ammonites characterized by such complex, repeatedly bifurcating rib bundles (Pavlow in Pavlow and Lamplugh, 1892, p. 476, 477; Pl. XV (VIII), fig. 2).

The ontogenetic development of the ornament in *Ringnesiceras* and *Elleficeras* (see their generic descriptions for further details) indicates that the relatively simple and constant simbirskitinid rib bundle consisting of two to four monodichotomously to fasciculately branching secondary ribs attached to a straight and fairly long primary rib is but a modification of juvenile rib bundles of *Polyptychites* s. str. The simbirskitinid primary arises by straightening and elongation of the polyptychitinid primary rib and addition of a more or less prominent *tubercle* (a rounded, sharptopped elevation) at its branching point. The simbirskitinid ribbing habit was already adequately described and illustrated by Pavlow (in Pavlow and Lamplugh, 1892, p. 499; Pl. XVII, figs. 3, 4, 8, 15) and does not require further comments.

The position of the first ribs to appear on the early juvenile whorls of Polyptychitinae is taxonomically important. In *Siberiptychites*, *Astieriptychites*, and probably in other high Boreal genera as well, they are at first restricted to the venter and the outer parts of the flank while in *Polyptychites* s. str. they are first restricted to the adumbilical parts of the flanks and umbilical shoulder (Klimova, 1978, 1981). In combination with the restriction of constrictions to the members of the high Boreal evolutionary development of the Polyptychitinae, this morphological feature appears to be a particularly stable and hence taxonomically high ranking one.

The sequences of ontogenetic sculptural stages were found to be much less variable and less repetitive features than the individual sculptural growth stages. Therefore, they provide a way to unravel the bewildering array of only homoeomorphically similar individual sculptural patterns. This rather complex ontogenetic development of the polyptychitinid sculpture exhibits pronounced differences between the high Boreal and European evolutionary developments of the subfamily. Therefore, it will be described and taxonomically evaluated below in the appropriate taxonomic sections (see p. 136-139, Figures 51a-51c for further details).

Most of the sculptural elements of the Polyptychitinae shell, such as the ribbing habit, the tendency to lose the sculpture (completely or in part) on the adult ultimate and more rarely the adult penultimate whorl, the presence or absence of umbilical bullae, and the presence or absence of forward bends of supplementary ribs on the venter, vary strongly and irregularly within the subfamily. As in the Craspeditidae (see Jeletzky, 1979, p. 7), the evolution of these features in their individual lineages appears to be dominated entirely by "reversible morphological shifts" as defined by Jeletzky (1955, p. 483, Text-fig. 1; 1965a, p. 4, 5) in Belemnitellidae and *Buchia*. Furthermore, similar to identical sculptural types tend to reappear and to disappear haphazardly in different lineages of the subfamily. This "iterative" mode of evolution of the sculpture strongly complicates the identification of specific and higher taxa of Polyptychitinae on this feature alone. For example, the bidichotomous sculpture characteristic of advanced representatives of Northwest European *Dichotomites* s. str. (e.g. Kemper, 1978, Pl. 13, fig. 1; Pl. 14, fig. 1; Pl. 15, figs. 1, 2; Pl. 16, figs. 1, 2a) recurs in the same growth stages of only distantly related members of late Valanginian Simbirskitinae (*e.g. Ringnesiceras* s. str. and *Elleficeras*; see Pl. 57, fig. 2, Pl. 58, figs. 4A, 4B; Pl. 60, fig. 3B). Furthermore, the same is true of the polyptychous and heteroptychous types of bundles of the large cotype of *Polyptychites polyptychus* (Keyserling, 1846, Pl. 21, fig. 1) and the extreme representatives of *P. pavlowi* (Pavlow in Pavlow and Lamplugh, 1892, Pl. XV, fig. 2) and *P. keyserlingi* (Koenen, 1902; Pl. XLIX, fig. 1). The recurrence of this mode of bundling in the intermediate and adult growth stages of *Ringnesiceras* has led to the erection of the species *R. (R.) pseudopolyptychum* Kemper & Jeletzky 1979.

The marked forward bend of supplementary ribs on the venter of European *Dichotomites* and *Prodichotomites*, that distinguishes them from the ancestral *Polyptychites* s. str. and related early Valanginian genera, is only diagnostic within that province. A similar medioventral forward bend of supplementary ribs occurs in the only indirectly related high Boreal polyptychitinid genus *Amundiptychites* that co-exists there with true *Prodichotomites* and *Dichotomites* (compare Pl. 47, fig. 1C; Pl. 48, fig. 1B; Pl. 53, figs. 2C, 2D; Pl. 63, figs. 1A, 1B with Pl. 49, fig. 3C or Pl. 23, figs. 1B, 2C; Pl. 24, figs. 3B, 4B and Pl. 25, fig. 1B). Furthermore, a similar forward bend occurs in even more distantly related late Valanginian representatives of Simbirskitinae (*e.g. Ringnesiceras* s. str. and *Elleficeras*; see Pl. 51, fig. 1D; Pl. 52, fig. 2C; Pl. 57, fig. 1; Pl. 60, figs. 2C, 2D, 3C, 3D). This similarity, in combination with an equally close similarity of the cross-section and suture line of these high Boreal genera with those of true *Dichotomites* and *Prodichotomites*, resulted in their original assignment to the latter genera (e.g. Jeletzky, 1973; Kemper, 1975, 1977). These misidentifications were only corrected later (Kemper and Jeletzky, 1979) when the ontogenetic development of the ornament of *Amundiptychites*, *Ringnesiceras* and *Elleficeras* was studied in a greater detail.

Kemper (1978, p. 194) has already discussed the far-reaching homoeomorphy of the sculptural changes characteristic of the true early early Valanginian *Neocraspedites* s. str. with those of only indirectly related late representatives of mid- late Valanginian *Prodichotomites*. This homoeomorphy, combined with a far-reaching similarity of the whorl shape of the forms concerned, had already resulted in an erroneous use of the name *Neocraspedites* for these *Prodichotomites* species (e.g. Spath, 1924).

Other examples could be cited to demonstrate a frequent recurrence of similar to identical types of sculpture in only distantly related genera and species of Polyptychitinae and Valanginian Simbirskitinae. However, the above examples,and other examples provided in the description of the individual genera, amply illustrate the point and serve as a warning against relying unreservedly on a similarity of individual sculptural growth stages (especially the late ones) when trying to determine polyptychitinid and early simbirskitinid ammonites generically and subgenerically. As pointed out below in the taxonomic sections, there are many instances when only a close study of the entire ontogenetic development of their sculpture in combination with other morphological features permits a reliable identification and dating.

As already pointed out by Jeletzky (1965a, p. 39, Footnote; 1973, p. 73; 1979, p. 7) and Kemper (1978, p. 188 and unpublished), the situation is further aggravated by a common recurrence of morphologically similar to identical sculptural patterns in the Craspeditidae. These homoeomorphies have already caused long-lasting misidentification of the North American and North Siberian craspeditid *Homolsomites* with the largely European polyptychitinid *Dichotomites*.

Shell shape and proportions

Figure 10 elucidates the elements of the ammonite shell measured by the authors and the abbreviations used for them in the measurement tables throughout the text. In addition to the measurable shell elements shown in this figure, the following ratios have been used in these tables. The width of the umbilicus as a percentage of the shell diameter is listed in brackets behind the value of the umbilicus. The height of the whorl as a percentage of shell diameter is listed in brackets behind the value of the former (Wh). Finally, the width of the whorl as percentage of the shell diameter is listed in brackets behind the value of the former (Wth.).

In addition, the ratio of the whorl's height to its width as a percentage is used in the measurement tables of species described by J.A. Jeletzky but not in those of species described by E. Kemper.

The degree of involution of the shell is described as follows:

	Umbilicus as % of shell diameter (D).
Very involute	1 - 8%
Involute	9 - 17%
Moderately involute	18 - 34%
Moderately evolute	35 - 60%
Very evolute	Over 60%

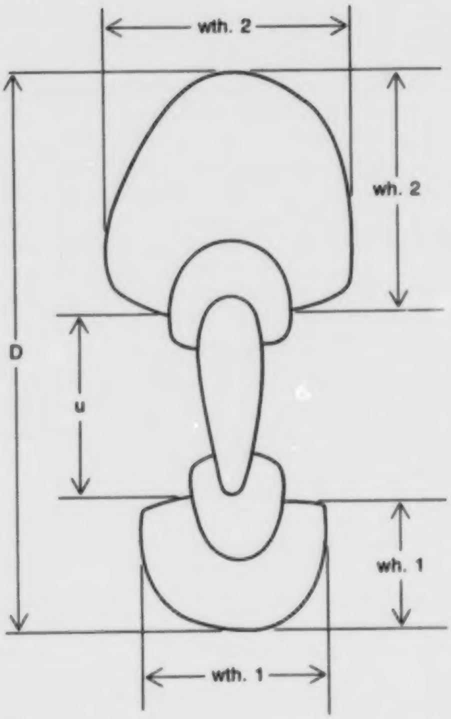

Figure 10. Principal measurements of the ammonite shell (in mm) and their designations. D — Shell diameter; u — Width of the umbilicus measured between the opposed points on the umbilical rim; Wh — Whorl height; Wh.1 — Whorl height on the early half of the whorl; Wh.2 — Whorl height on the oral half of the whorl; Wth — Whorl thickness; Wth.I — Whorl thickness on the early part of the whorl; Wth.2 — Whorl thickness on the oral part of the whorl.

The whorl shape and proportions are extremely variable within the Polyptychitinae. Furthermore, the same morphological trends are repeated in the evolution of its independent, often geographically and biochronologically remote lineages. Two of these iterative trends are prevalent in polyptychitinid evolution. The first trend consists in a gradual widening and lowering of the whorl's cross-section. It leads from slender, discus-like cross-sections exemplified by those of *Paratollia* and *Bodylevskites* to hoof-shaped, wider than high (i.e. *Polyptychites*-like) cross-section and then to a low-arched, much wider than high and angular-shouldered (i.e. *Euryptychites*- or *Cadoceras*-like) cross-section. So far as known, it always ends with the latter cross-sections. This trend recurs several times in the evolution of the Polyptychitinae. It produced the true *Euryptychites* in the early Valanginian of Northwest Europe and East Greenland, the superficially similar *Hollwediceras* n. gen. in the early/late Valanginian boundary beds of the Lower Saxony Basin and the superficially similar *Pseudoeuryptychites* in the early Valanginian of the high Boreal basins of Northern Siberia and Canada. All these only distantly and indirectly related *Euryptychites*-like taxa (see in their taxonomic descriptions for further details) were invariably lumped together prior to this study.

The second, equally prominent evolutionary trend of the whorl shape leads in the opposite direction. All lineages dominated by this trend lead from more or less hooflike, wider than high (i.e. *Polyptychites*-like) cross-sections to slender, subparallel-flanked and narrowly ventered ones. These end forms are always *Dichotomites*-like. However, they are also similar to the cross-sections of *Paratollia* and *Bodylevskites* with which the known evolution of Polyptychitinae started.

Kemper (1978, p. 191) has already described the operation of this trend in the evolution of the Lower Saxony representatives of *Polyptychites*, *Prodichotomites* and *Dichotomites*. However, it was recognized subsequently (see p. 90 for further details) that *Dichotomites* s. str. is not a direct descendant of *Prodichotomites* but a homoeomorphically similar end phase of another evolutionary lineage that begins with much sturdier, *Polyptychites*-like ancestors in the early-late Valanginian boundary beds of Northern Siberia. Yet another, entirely independent evolutionary trend leading toward a *Dichotomites*-like whorl cross-section was operative in the *Siberiptychites* lineages of North Siberia. This early Valanginian trend also led from *Polyptychites*-like *S.* (*S.*) ex gr. *stubendorffi* to almost entirely *Dichotomites*-like "*Siberiptychites*" *politus* Voronets 1962 and allied forms of the *Polyptychites michalskii* Zone. The same trend toward the *Dichotomites*-like (or *Prodichotomites*-like) cross-sections was apparently operative in the Sverdrup Basin lineage leading from the earliest known, *Polyptychites*-like *Ringnesiceras* s. str. toward *Elleficeras* and in the principal lineage of *Ringnesiceras* culminating in *R. tozeri* (Kemper and Jeletzky, 1979, p. 13, Fig. 8 and below). Finally, this trend is apparent in the early early to mid- early Valanginian polyptychitinid lineage(s) that begins with the *Polyptychites*-like *Propolyptychites* forms and ends with the *Prodichotomites*-like *Neocraspedites* ex gr. *semilaevis* (see Figure 11 and p. 37, 38 for further details).

Like the homoeomorphic *Euryptychites*-like polyptychitinids, the various *Dichotomites*- and/or *Prodichotomites*-like end forms were almost invariably lumped together as such prior to this study.

Conclusions

The above description of the principal features of shell morphology of the Polyptychitinae and Valanginian Simbirskitinae reveals that they are all extremely variable on the generic and specific levels. Furthermore, the evolution of all these morphological features is extremely repetitive in all presently known polyptychitinid and simbirskitinid lineages. This results in a repeated emergence of homoeomorphically similar end forms in many indirectly related and geographically remote lineages.

Though the adult external suture line is a considerably more stable feature in time and in space than either the shell's sculpture or the shell's shape and proportions, it is also affected by the iterative mode of evolution that is so characteristic of polyptychitinid and early simbirskitinid ammonites. Jeletzky's (1965b, p. 2; 1979, p. 3, Figure 1) claim of its taxonomic superiority to the sculpture and shell's shape is, therefore, an overestimation.

Conversely, the shell's sculpture was found to be more valuable than was thought by Jeletzky (l. cit.). In spite of the extreme variability of most sculptural features and their pronouncedly recurrent mode of evolution, some of them proved to be distinctive on the generic level. This is true, for example, of constrictions and the mode of initial appearance of ribbing (see below in the description of *Siberiptychites*). Furthermore, the ontogenetic sequences of sculptural patterns were found to be stable and unique in a number of polyptychitinid and early simbirskitinid lineages (e.g. in *Siberiptychites*, *Polyptychites* s. str., *Dichotomites* and *Ringnesiceras*; see their descriptions for further details).

The whorl shape and proportions were also found to be more valuable taxonomically than was thought by Jeletzky (l. cit.). Though they are even more variable and evolutionarily repetitive than the majority of sculptural patterns, some of their ontogenetic sequences were found to be rather stable and distinctive. The distinctions of ontogenetic development of the whorl shape of *Amundiptychites* from that of the homoeomorphic genera *Dichotomites* and *Prodichotomites* is a good example.

This re-evaluation of the comparative taxonomic value of the various morphological features of the shell indicates that it is not possible to use any of them individually as a key for unravelling the extremely complex evolutionary development of the Polyptychitinae and Valanginian Simbirskitinae to reclassify them. Though the adult external suture line remains the most valuable individual feature presently available, it definitely falls short of that role. The same is also true of the sculptural features. Hence it is necessary to investigate minutely and use taxonomically all morphological features. Furthermore, one has to consider seriously the stratigraphic and geographical positions of the forms studied and their intergradation (or lack thereof) with older and younger, closely similar shells confined to the same marine basin. A definitive generic and/or specific identification of fragmentary or poorly preserved specimens that display only some morphological features is inadvisable. It is apt to result in their gross misidentification and erroneous dating. The definitive identification of juvenile specimens in the absence of associated adult shells is considered to be particularly hazardous. In the writers' opinion, only reasonably well preserved shells consisting of several whorls (or their fragments) can be safely identified generically and specifically.

PALEONTOLOGICAL DESCRIPTIONS

Family Olcostephanidae Haugh 1910

Remarks. The family Olcostephanidae Haugh 1910 is interpreted essentially as it was by Wright (in Arkell et al., 1957, p. L344-L350) but considerably more broadly than by Khimiashvili et al. (1958, p. 94-95, Fig. 78). It seems unreasonable to split the subfamily Polyptychitinae Spath 1924 off the directly ancestral subfamily Spiticeratinae Spath 1924 and to give it a full family rank. It is even less justifiable to give a full family rank to the Simbirskitinae Spath 1924 after its close affinities and direct descendant-ancestor relationships with Polyptychitinae Spath 1924 were demonstrated by the discovery of *Ringnesiceras* in the Upper Valanginian rocks of the Sverdrup Basin and Pechora Region of the U.S.S.R. Therefore, the family Olcostephanidae Haugh 1910 is here taken to include the subfamilies: Spiticeratinae Spath 1924; Olcostephaninae Haugh 1910 s. str.; Polyptychitinae Spath 1924; and Simbirskitinae Spath 1924.

Subfamily Polyptychitinae Spath 1924

Diagnosis. Moderately slender to very depressed shells ranging from platicones to cadicones. Prorsiradiate to subtransversal supplementary (secondary to tertiary and more rarely quaternary) ribs spring from subtransversal primary ribs on juvenile whorls and from umbilical bullae on advanced to/or adult whorls. Intercalated ribs and bundles may be common. The supplementary ribs tend to form relatively simple monodichotomous to trivirgatitpartitous bundles on juvenile whorls and much more complex polyptychous, heteroptychous, bidichotomous, tridichotomous, quadri- to polyvirgatitpartitous and quadri- to polyfasciculate bundles on advanced to adult whorls. Lateral and ventro- lateral bullae and tubercles absent. Innermost whorls smooth. Constrictions present in some lineages but absent in others. Adult external suture line subradial to distinctly ascendant in the lateral and, sometimes, outer auxiliary part but always feebly to markedly descendant (or retractive) in most or all of the auxiliary part. It includes two to five clearly differentiated auxiliary lobes separated from each other by one or more much smaller lobules.

Time range. Apparently restricted to the Valanginian stage of the Boreal Realm and northern marginal regions of the Tethyan Belt. However, may possibly range down into the late Berriasian (e.g. *Peregrinoceras* sensu Casey 1973).

Discussion. The morphological distinctions of Polyptychitinae from the most closely allied and commonly homoeomorphic Olcostephanidae subfamilies and the only indirectly allied but pronouncedly homoeomorphic Craspeditidae have already been discussed in the sections on methods and terminology.

According to Wright (in Arkell et al., 1957, p. L348), Kemper (1978, p. 180) and Jeletzky (1979, p. 4) the subfamily Polyptychitinae descended from the Tethyan Olcostephanidae via the Berriasian representatives of *Spiticeras*. This idea is favored by the writers, in spite of a subsequent change of opinion by Wright (1980, p. 161). These descendants of *Spiticeras* must have migrated into the marginal marine basins of the Atlantic Province of the Boreal Realm in the latest Berriasian or earliest Valanginian. There, and specifically in Northwest and Central Europe, they flourished and began to evolve independently from the Spiticeratinae. In the earliest known, typogenetic (Schindewolf, 1947) phase of their evolution, that lasted through the early early Valanginian (= *Platylenticeras*-Beds), the Northwest European Polyptychitinae produced the genera *Paratollia* sensu Casey 1973, *Propolyptychites*, *Neocraspedites*, *Euryptychites* and *Polyptychites* s. str.[1]). All these genera are inferred to be descendants of *Bodylevskites* ex gr. *pumilio* (Vogel 1959) (see the description of *Bodylevskites* for further details). *Bodylevskites* ex gr. *pumilio* are also inferred to be ancestral to all lineages of high Boreal Polyptychitinae described in the second part of this paper (see p. 21 and Figure 11).

The oldest recorded Polyptychitinae are known from East Greenland (P.F. Rawson, personal communication), the Island of Helgoland and the Lower Saxony Basin. The finds of Helgoland (Hiltermann and Kemper, 1969) indicate their remarkably frequent occurrence in the system of marine basins hidden beneath the North Sea. Therefore, they are believed to have migrated from there into the Lower Saxony Basin (Figure 11).

The Polyptychitinae are still very rare in the oldest marine beds of the Lower Cretaceous (i.e. the *Platylenticeras*-Beds) in the Lower Saxony Basin. Therefore, our knowledge of their earliest evolutionary development there remains fragmentary. All presently available data were summarized by Kemper (1976). A frequent occurrence of homoeomorphic forms complicates the taxonomic evaluation of poorly to incompletely preserved fossil material derived from these beds.

Northwest German and Related Northwest European Taxa

Genus *Peregrinoceras* Sazonova 1971 sensu Casey 1973

Type species. This insufficiently understood late Berriasian genus is not represented in the Northwest German material studied. However, a critical appraisal of the taxonomic position and phylogenetic ties of some English ammonites placed into it by Casey (1973) is attempted here.

Casey (1973, p. 256) assigned ammonites which dominate the faunas of the topmost Spilsby Sandstone, basal Claxby Beds (Hundleby Clay) and lower D Beds of the Speeton Clay to the genus *Peregrinoceras* Sazonova. One of these species — *Peregrinoceras albidum* Casey 1973 — was designated as the zonal index fossil of these beds. The suture line of these English ammonites figured by Casey (1973, p. 255, Fig. 6h) has an expressly non-craspeditid character while matching closely those of *Paratollia* and *Propolyptychites*. These *Peregrinoceras*? forms must consequently be placed into the Polyptychitinae. The suture line of *Olcostephanus pressulus* is insufficiently understood (Sazonova, 1971, 1977), but this type species of *Peregrinoceras* is suspected of being a representative of the Graspeditidae because of the almost certainly craspeditid (*Surites*-like) character of the external suture line of another Central Russian ammonite described by Sazonova (1971, p. 69, 70, Pl. XVII, figs. 2, 2a; 1977, Pl. XXI, fig. 4) as *Peregrinoceras ramosum*. Should this be the case, this generic name would not be applicable to the English species and a new generic name would have to be introduced. Alternatively, it may be

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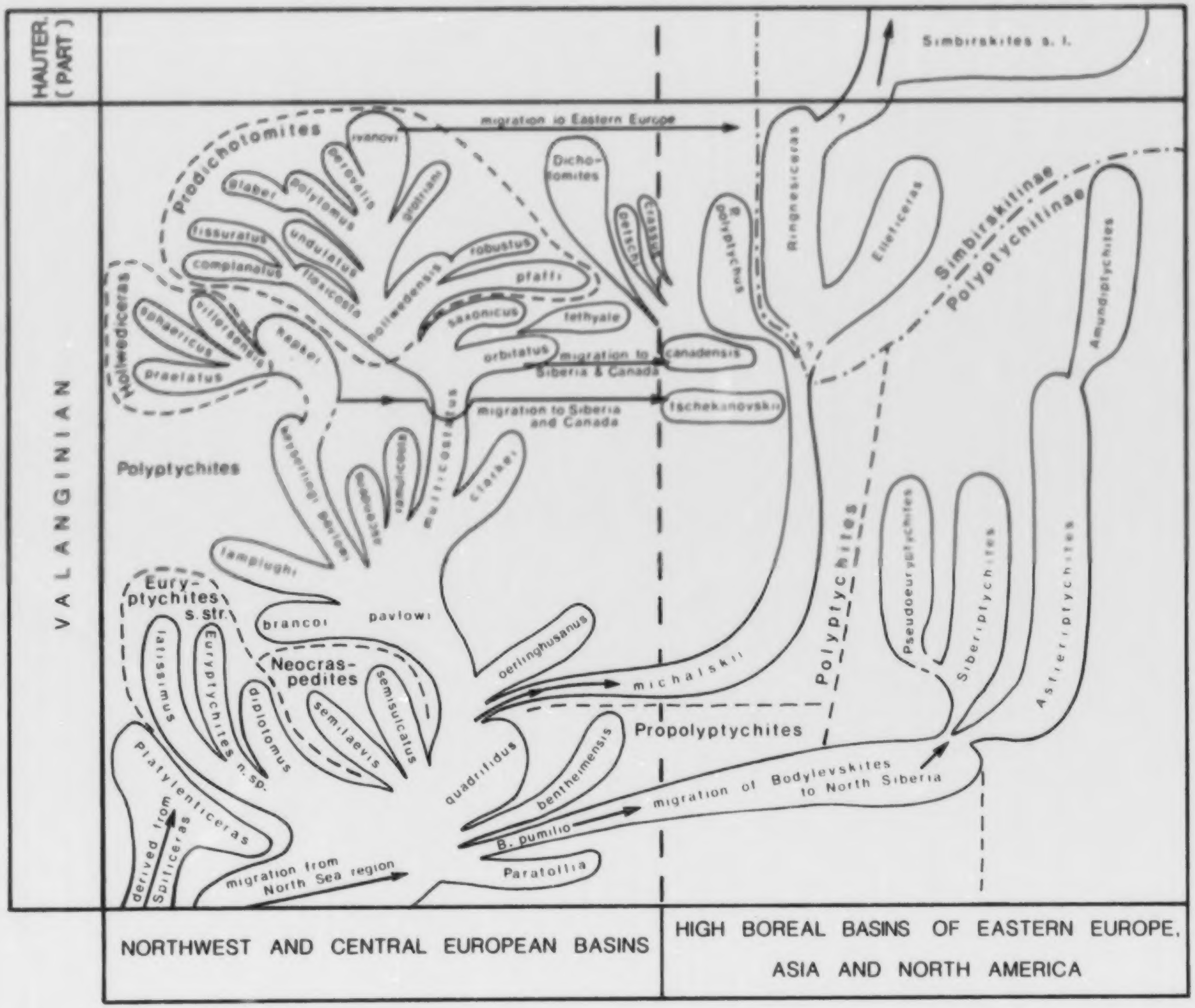
[1] As noted by Kemper (1976, p. 33, 34, expl. of Pl.12, fig. 4), *Platylenticeras* appears to be a direct descendant of *Spiticeras*. Therefore, it is here considered to be an aberrant offshoot of Spiticeratinae that died out without an issue.



HAUTER. (PART)
VALANGINIAN
Simbirskites s. l.
?
migration to Eastern Europe
Prodichotomites
ivanovi
perovalis
grotriani
glaber
polytomus
fissuratus
undulatus
complanatus
flexicosta
hollwedensis
robustus
pfaffi
Dichotomites
petschi
crassus
Hollwedicer as
sphaericus
villersensis
praelatus
saxonicus
tethyale
orbitatus
migration to Siberia & Canada
canadensis
migration to Siberia and Canada
tschekanovskii
Polyptychites
keyserlingi
multicostatus
clarkei
ramulicosta
lamplughi
Eury-ptychites s. str.
brancoi
pavlowi
latissimus
Euryptychites n. sp.
diplotomus
Neocras-pedites
semilaevis
semisulcatus
oerlinghusanus
michalskii
Propolyptychites
quadrifidus
bentheimensis
B. pumilio
Paratollia
Platylenticeras
derived from Spiticeras
migration from North Sea region
migration of Bodylevskites to North Siberia
R. polyptychus
Ringnesiceras
Elleticeras
Simbirskitinae
Polyptychitinae
Amundiptychites
Polyptychites
Pseudoeuryptychites
Siberiptychites
Astieriptychites
NORTHWEST AND CENTRAL EUROPEAN BASINS
HIGH BOREAL BASINS OF EASTERN EUROPE, ASIA AND NORTH AMERICA

Figure 11. Inferred phylogenetic relationships and interregional migrations of the Valanginian Polyptychitinae and Simbirskitinae.

necessary to assign them to the genus *Bodylevskites* to which they are morphologically similar in several respects. This problem cannot be settled definitively at present: for now, the species group is assigned to *Peregrinoceras* sensu Casey.

Peregrinoceras sensu Casey 1973 is characterized by a combination of a *Tollia*-like sculpture with an early polyptychitinid suture line, which is described in a greater detail below in the description of the genus *Paratollia*. This suture line differs from that of *Bodylevskites* in the same features as it does from that of *Paratollia*. The *Tollia*-like sculpture of *Peregrinoceras* sensu Casey 1973 has slender primary ribs which split into secondary ribs only in mid-flank. Neither a subdivision of primaries into secondary ribs in the proximity of the umbilicus nor typical umbilical bullae are yet present in the genus. Rib bundling in the proximity of the umbilicus is, however, typical of other early Polyptychitinae genera, including *Paratollia* Casey 1973. These two sculptural types are connected by transitions (Casey, 1973, Pl. 5, fig. 5a; Pl. 10, fig. 3).

Peregrinoceras sensu Casey 1973 is inferred to be the rootstock of the other Polyptychitinae, presumably including the North Siberian *Bodylevskites* Klimova 1978. Its eastern English representatives could be included in *Bodylevskites*, except for the apparent absence of constrictions. The superficially similar genera *Costamenjaites* Sazonova 1971 and *Borealites* Klimova 1969 possess a typical craspeditid suture line with four to five auxiliary lobes (Klimova, 1969, p. 129, 130, Figures 1v, 3b; Jeletzky, 1973, 1979, p. 11, 13, Figures 5-6). Therefore, they are homeomorphic representatives of the family Craspeditidae. The same applies also to *Tollia* Pavlow 1914 and *Neotollia* Shulgina 1969, which are synonymous according to Jeletzky (1979, p. 46-48). These two genera have, furthermore, a sculpture which differs sharply from that of *Peregrinoceras* sensu Casey 1973. Therefore, they cannot be easily confused with it even in the absence of a suture line.

Bodylevskites Klimova 1978

Type species. ***Bodylevskites harabuliensis*** Klimova 1978.

Diagnosis. The original diagnosis of Klimova (1978, p. 50, 51) is as follows (translation from Russian by J.A. Jeletzky): "Shell of a discoidal shape. The flanks and the siphonal side are flattened to a greater or lesser degree. The cross-section varies from oval-rectangular to subtrapezoidal. The umbilicus is fairly shallow, step-like and either moderately narrow or moderately wide. The umbilical wall is perpendicular and smooth. The sculpture begins on the umbilical shoulder. The umbilical ribs of the inner whorls either subdivide forming dichotomous or trichotomous bundles starting from a solitary virgation point or remain single. Numerous intercalated ribs are present. They include some dichotomous ribs. As the shell grows, the umbilical ribs acquire the appearance of elongated low nodes. The sculpture of the lower half of the flanks either (progressively; translator's remark) fades away or loses much of its relief. Consequently a smooth zone forms between the umbilical and external ribs. The coefficient of branching (of umbilical ribs; translator's remark) is 4 to 6. It increases with the growth of shell. The ribs are strengthened on the siphonal side. The length of the body chamber exceeds one whorl. The formula of the suture line is $V_1\ V_1\ UU^1\ U^2_1\ U^3_1\ U^4_1 : U^4_1\ U^3_1\ U^2_1\ ID$. The tops of saddles of the external part of the suture line are situated on a line that parallels the shell's radius."

Type area. Central part of North Siberia (Anabar-Khatanga Basin).

Age. Lower (?including the basal) part of the lower Valanginian substage. Subzone of *Temnoptychites simplicissimus* of the regional North Siberian *Temnoptychites syzranicus* Zone (see Klimova, 1981, p. 74; Gol'bert et al., 1981, p. 56, 57 for further details) that was introduced to replace the basal Valanginian *Tollia klimovskiensis* Zone of Saks and Shulgina (1969, 1974, p. 145, Corr. Table). *Platylenticeras*-Beds and basal *Polyptychites*-Beds of the Lower Saxony Basin. D4 Bed of Speeton Clay.

Geographical range. Central part of northern Siberia and Northwest Europe (Lower Saxony Basin and East England).

Discussion. The discovery of *Bodylevskites* in the lower (?including the basal) lower Valanginian rocks of North Siberia that underlie those containing the bulk of *Siberiptychites* and *Astieriptychites* and all North Siberian representatives of *Polyptychites* (Klimova, 1981, p. 74; Gol'bert et al., 1981, p. 56, 57, Tables 3, 4) provided for the first time a credible connecting link between the numerous and typical Polyptychitinae that inhabited the early Valanginian epicontinental basins of North Western and North Central Europe and the morphologically aberrant, endemic Polyptychitinae (e.g. *Siberiptychites*, *Astieriptychites* and *Amundiptychites*) that inhabited the high Boreal (or Arctic) early Valanginian basins. This almost exclusively Central Siberian genus is described in the chapter dealing with the Northwest German Polyptychitinae because it is not known to occur in Arctic Canada (or for that matter anywhere else in Arctic North America) while being present in Northwestern Europe. In the latter region it is represented by the previously misinterpreted "*Polyptychites*" *pumilio* Vogel 1959, that is redescribed and re-evaluated below.

As it is known now, *Bodylevskites* Klimova 1978 differs from *Siberiptychites* first of all in the presence of only two auxiliary lobes (instead of at least three) in its halfgrown to adult shells (Klimova, 1978, Figures 4, 5). Furthermore, the auxiliary part of its external suture line is pronouncedly retractive (or descendant) according to Klimova's (1978, Figures 4, 5) drawings. Finally, *Bodylevskites* has a slender (higher than wide), rounded-rectangular to subtrapezoidal halfgrown to adult cross-section (Klimova, 1978, Figures 1-9, 2-3, 2-4; Plate 1, fig. 2b, Pl. 2; figs. 2b, 3a, 4a, 5a) that only resembles that of "*Polyptychites*" *pumilio* Vogel 1959, eastern English ammonites assigned to *Peregrinoceras* by Casey (1973), and some juvenile representatives of *Siberiptychites* (e.g. Pavlow, 1914, Pl. V, figs. 6b, 7b). The *Euryptychites*-like to sphaeroidal cross-section of early and halfgrown whorls of *Bodylevskites* (Klimova, 1978, Figures 1-1 to

1-8 inclusive, 2-1 and 2-2; Pl. 1, fig. 1a) is similar to the equivalent growth stage of "*P.*" *pumilio* (see Vogel, 1959, Figures 19, 20) and to the first *Euryptychites*-like growth stage of *Siberiptychites*. In combination with the restriction of *Bodylevskites* to beds where the representatives of the genera *Siberiptychites* (apparently *S. (S.) stubendorffi* only) and *Astieriptychites* make their first appearance, these similarities and differences in ontogenetic development indicate that the generally younger *Siberiptychites* and *Astieriptychites* arose very rapidly (an evolutionary burst) from *Bodylevskites* via a generally palingenetic (or recapitulational) evolutionary mode. This conclusion is supported by the characteristic presence of frequent constrictions in all three genera and their coexistence in the Anadyr'-Khatanga Basin of North Siberia. The fact that *Siberiptychites* and *Astieriptychites* appear earlier in that basin than in any other Boreal basin where they occur points in the same direction.

The inferred palingenetic (or recapitulational) transmutation of *Bodylevskites* into *Siberiptychites* s. str. must have consisted in the relegation of its characteristic half-grown to adult whorl shape and proportions to the late juvenile growth stages (i.e. the *Bodylevskites*-like growth stage observed in *S. (S.) stubendorffi* and *S.* (*P.*) *middendorffi*). This process must have been combined with the addition of a new, terminal growth stage to its ontogeny, that was characterized by the *Polyptychites*-like whorl shape and proportions. The essentially parallel-running palingenetic transformation of the external suture line must have consisted of the addition of a new, terminal growth stage featuring the appearance of the third auxiliary lobe in its adumbilicalmost part and the adventral displacement of the second auxiliary (i.e. of the lobe U_2^1 of Klimova, 1978, p. 55, Figs. 3, 4, 6) onto the inner part of the flank. Finally, the originally adult, refined and closely spaced, almost to nonbullate, dichotomous to trichotomous ribbing habit of *Bodylevskites* with the characteristically flexuous, forward inclined appearance of supplementary ribs and their pronounced forward bends on the venter (see Klimova, 1978, p. 50, 51; Pls. 1, 2) must have also been relegated to the late juvenile to early intermediate growth stages of the subgenus *Siberiptychites* s. str. (i.e. its simple dichotomous and *Bodylevskites*-like sculptural stages; see p. 136, Figures 51a-51c for further details). Here also new, terminal growth stages characterized by essentially *Polyptychites*-like sculpture (i.e. the predominantly trivirgatitpartitous and the predominantly quadripartitous sculptural phases) must have been added. In contrast, the first *Euryptychites*-like stage of the whorl shape and the numerous constrictions characteristic of *Bodylevskites* (Klimova, 1978, p. 51; Pls. 1, 3; p. 54, Figs. 2-1 to 1-6 inclusive) were recapitulated in the subgenus *Siberiptychites* s. str. without any apparent abbreviation.

The considerable increase of the adult shell size characteristic of *S. (S.) stubendorffi* (apparently the immediate descendant of *Bodylevskites*) as compared with that of *Bodylevskites* indicates that the above evolutionary changes did not actually involve a relegation of the features concerned to the earlier growth stages. Instead, additional morphological growth stages were being added to the ontogeny of *Bodylevskites* during its transmutation into *Siberiptychites* s. str.

Such palingenetic transmutation must have also characterized the evolutionary development of *Astieriptychites* out of *Bodylevskites* as these two genera differ in essentially the same adult morphological features as *Siberiptychites* s. str. (i.e. *S. (S.)* ex gr. *stubendorffi*) does from *Bodylevskites*.

Bodylevskites pumilio (Vogel 1959) occurs in the *Platylenticeras*-Beds and the basal part of the *Polyptychites*-Beds of Northwestern Germany and in the equivalent beds of the Speeton Clay in East England where it appears to be totally isolated phylogenetically from the younger representatives of Polyptychitinae. However, its relatively primitive rather *Peregrinoceras*-like morphology and stratigraphic position in the lower lower (possibly basal) Valanginian beds suggests strongly its being the progenitor of the presumably slightly younger North Siberian representatives of the genus and hence of all the separate North Siberian development of the Polyptychitinae (Figure 11). This so far unique European representative of *Bodylevskites* probably descended from *Peregrinoceras* sensu Casey. If so, *B. pumilio* must have either acquired or retained the characteristic features of *Bodylevskites* (i.e. the presence of constrictions, strongly flexuous appearance of primary and supplementary ribs on the flank and the pronounced forward bends of supplementaries on the venter, etc.) that are totally absent in all other presently known early representatives of Polyptychitinae in Northwest and northern-central Europe. The totally isolated position of *B. pumilio* in that region indicates that this stock rapidly became extinct there and only survived in the Central Siberian basin (and possibly in other high Boreal basins) following its early (possibly earliest?) early Valanginian migration there.

Bodylevskites pumilio (Vogel 1959)

Pl. 7, figs. 7, 8; Pl. 8, fig. 5; Pl. 10, fig. 4; Pl. 27, fig. 3; Pl. 28, figs. 3, 6, 7; Figure 12.

Synonymy

1892	*Olcostephanus (Craspedites) fragilis* Pavlow, in Pavlow and Lamplugh, p. 475, 476; Pl. XIII, fig. 4 *(non* fig. 3).
1902	*Polyptychites euomphalus* Koenen, p. 85, 86; Pl. 55, fig. 7.
1902	*Polyptychites* juven. aff. *euomphalus* Koenen, p. 119; Pl. 55, fig. 8.
1902	*Polyptychites* juven. an *brancoi* Koenen, p. 137, Pl. 55, fig. 9.
1902	*Polyptychites* juv. an *ascendens* Koenen (in the text as *Olcostephanus* juv. n. sp. aff. *euomphalus* Koenen), p. 120, Pl. 55, fig. 10a, 10b.
1902	*Olcostephanus* sp. juv. an *gradatus* Koenen?, p. 85, 86, Pl. 55, figs. 13a, 13b and 14a, 14b.
1906	*Olcostephanus (Craspedites) fragilis* Danford, p. 104, Pl. XI, figs. 1, 1a.
*1959	*Polyptychites pumilio* Vogel, p. 494-520, Pl. 25-27 *(non* Pl. 26, fig. 2; pl. 27, fig. 12; Pl. 28, figs. 1-2, 3b-6).

1964 *Tollia pumilio* Kemper, p. 22, Pl. 1, fig. 5; Pl. 2, fig. 1.
1968 *Tollia pumilio* Kemper, p. 32, Pl. 5, fig. 4.
1973 *Polyptychites pumilio* Casey, p. 257.
1976 *Paratollia pumilio* Kemper, p. 34; Pl. 5, fig. 4.

Holotype. Specimen figured by Vogel (1959, p. 498, Pl. 26, figs. 1a, 1b): GIG, Type Cat. No. 553701, by original designation.

Locus typicus. Jetenburg near Bueckeburg.

Stratum typicum. Lower *Polyptychites* Beds, lower lower Valanginian.

Material. 11 specimens from Jetenburg-Bueckeburg (BGR, Hannover) and photographs of some (Speeton Clay) specimens in the Doyle collection.

Diagnosis. Very small species (adult shell diameter about 20 mm) with slender whorls. Some representatives exhibit constrictions. Sculpture fine and dense with ribs inclined forward (prorsiradiate) and forming forwardly directed bends on the venter. Primary ribs are slender and split into secondary ribs not lower than mid-flank. No polyptychitinid bundles are present.

Measurements (in mm).

Specimen	Shell Diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
GIG 553701 Holotype	16.5	4.5(27)	5.0(30)	7.0(43)	—	5.5
GIG 553702	22.5	5.5(24)	7.5(33)	9.5(42)	—	8.0
GIG 553703	17.5	4.0(23)	5.5(31)	7.5(43)	—	7.5
Geol. Inst. Tue. 1119/2	16.5	4.7(28)	4.7(28)	7.0(43)	—	6.0
GIG 553705	13.5	3.5(26)	4.3(32)	5.7(42)	—	—
GIG 553709	14.5	3.3(23)	5.0(34)	6.2(43)	—	—

Description. Small ammonites associated with *Platylenticeras* and early *Polyptychites*-species in the lower Valanginian of middle and northwestern Europe have been known for a long time. A mass occurrence of these forms was discovered in the lower *Polyptychites*-Beds at Jetenburg-Bueckeburg (Vogel, 1959). English representatives from Speeton were assigned to the Upper Jurassic group of "*Olcostephanus (Craspedites) fragilis* Trautschold" by Pavlow and Lamplugh (1892). Koenen (1902, p. 85, 96, 118) interpreted German examples from the Jetenburg locality as "juveniles of *Polyptychites*" and assigned them to several species (see synonymy). Vogel (1959) monographed the group and interpreted it as a dwarf species of *Polyptychites*. He utilized about 600 specimens, most of which are in the collection of the Geological Institute in Goettingen. He did not recognize the species outside NW Germany. However, in addition to the English examples figured by Pavlow and Lamplugh (1892), J.C. Doyle possesses a nice collection of these small ammonites from Speeton where they were found in the upper D5 and D4 Beds. These ammonites are also associated with *Platylenticeras* and early *Polyptychites*-species at Speeton.

It happens only rarely that one species alone becomes a subject of a complete monograph, as happened here in Vogel's (1959) study. Because of the comprehensive nature of his description, only the most important morphological properties of *B. pumilio* will be pointed out here.

The whorls are slender and usually somewhat higher than wide. Their shape in cross-section is shown in Vogel's (1959, Figure 19a) drawings. The umbilicus is shallow and moderately involute (23 to 28%); its walls are gently inclined. The presence of constrictions is the most outstanding feature, as these do not occur at all in other northwest European Polyptychitinae *Polyptychites*, *Prodichotomites* and *Dichotomites*. Vogel (1959, p. 512) found one constriction at the end of the first whorl in all suitably preserved specimens. The time of disappearance of these constrictions in the course of the ontogeny varies. Only a few specimens (not more than about 25% of the material studied) continue to exhibit constrictions on the penultimate or even the ultimate whorl. The bulk of them lack constrictions already at the whorl diameter of 6 mm. The number of constrictions is also variable. Vogel (1959, Pl. 26, fig. 5a) figured a specimen which exhibits a solitary constriction on the ultimate whorl. Another (BGR, kv 355; Pl. 8, fig. 5) has no less than 3 constrictions concentrated on one of its half whorls. This extraordinary variability in number of constrictions may be interpreted either as reflecting the initial highly variable phase of their appearance in the rootstock of *Bodylevskites* or as a phenomenon of their decline in the course of evolution of the European lineage of Polyptychitinae. Because of the completely isolated position of *B. pumilio* in Europe, its apparently more primitive character as compared with the North Siberian representatives of the genus (see below), and its apparently close morphological and ?phylogenetical relationships with the English *Peregrinoceras* sensu Casey, forms that appear to be devoid of constrictions, the first alternative appears to be much more probable.

Vogel (1959, Figure 13; this paper Figure 12) has investigated the variability of the suture line. The external suture line is polyptychitinid, only slightly ascendant and rather primitive in the morphology of all its elements. It has only two auxiliary lobes. Judging by Klimova's (1978, Fig. 3-6) drawings, the lobes of *B. pumilio*'s suture are considerably wider, shorter and less denticulated than in North Siberian representatives of *Bodylevskites*. Furthermore, the suture of *B. pumilio* lacks the pronouncedly suspensive orientation of the auxiliary part that is characteristic of the North Siberian forms. All these features are consistent with the interpretation of *B. pumilio* as the most primitive representative of *Bodylevskites* known. Its relatively much smaller adult size appears to represent yet another primitive feature.

The shell is sculptureless initially, approximately to whorl diameters of 8 to 10 mm. Fine primary ribs appear thereafter, which are prorsiradiately oriented and sinuously to biconcavely bent. A very refined ribbing appears simultaneously on the ventral half of the whorls.

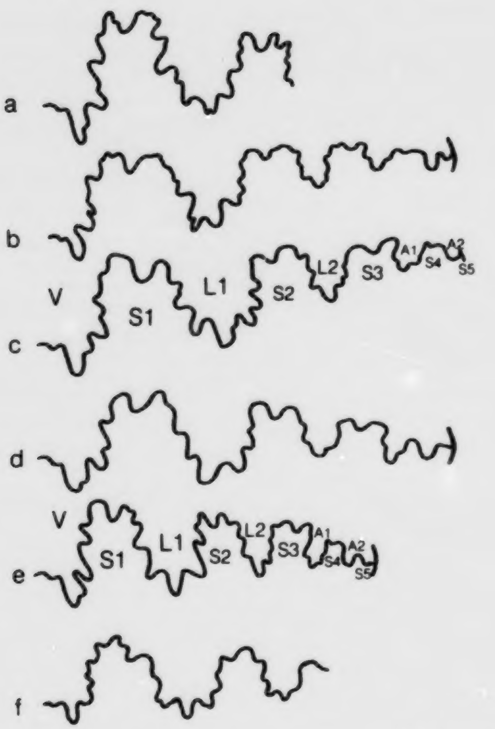


Figure 12. Variability of the adult external suture line of *Bodylevskites pumilio* (Vogel, 1959). From: Vogel, 1959, p. 509, Text-fig. 13. Locality: Bueckeburg-Jetenburg, Northwest Germany. Early early Valanginian. The whorl height measures approximately 4 mm and the drawings are enlarged accordingly.

Only a few of these secondary ribs branch from the primary ribs: most are simply intercalated between the latter.

The sculpture becomes more pronounced in the following growth stage, which extends to the adult mouth opening. However, it continues to consist of very fine individual elements. The primary ribs become somewhat stronger expressed in the proximity of the umbilicus. Their number on the last whorl is about 20. Their prorsiradiate inclination varies, but is strongly expressed in most specimens. Most of the secondary ribs of this growth stage branch off the primary ribs. They form quasifasciculate bundles and bend more or less forward on the venter. In some of the specimens the sculpture is weakened in a narrow zone situated in the middle of the flank just as it is in the North Siberian representatives of *Bodylevskites*. A remarkable decrease in the number of ribs per bundle occurs in the adult. Only bifurcating ribs are present in the latest growth stage in some of the specimens (Doyle's collection) from the middle part of D4 Bed of Speeton. This reduction does not go that far in the material from Jetenburg-Bueckeburg where the adult ribbing habit becomes irregular and at the same time variable (Vogel, 1959, Pl. 26). *B. pumilio* also includes almost smooth variants (Vogel, 1959, Pl. 26, figs. 6-8).

Affinities and differences. The most obvious distinction of *B. pumilio* from other *Bodylevskites* species is its insignificant shell dimensions combined with a relatively narrow umbilicus. Similar small species are, furthermore, unknown in other genera of the Polyptychitinae and constrictions are absent in all other European representatives of Polyptychitinae. Other distinctive features include the more primitive, relatively simplified appearance of its suture line and its subradial orientation.

Vogel did not differentiate consistently between *Bodylevskites* specimens and juvenile *Polyptychites*. Specimens of the latter were illustrated as *B. pumilio* on his plate 26 (fig. 2), plate 27 (fig. 12) and plate 28 (figs. 1-2, 3b-6). An impressive example of the distinctive morphology of the juvenile shells of *Polyptychites* is provided by the figures of plate 55 in Koenen (1902). In spite of the contradictory data provided by Vogel (1959, p. 494) one can see that figures 7-10 and 13-14 represent *B. pumilio* while the figures 5, 6, 11, 12 represent juvenile specimens of *Polyptychites*. The latter remain smooth to a shell diameter of about 10 mm. Then they develop a typical polyptychitinid ribbing habit with short primary ribs which split into secondary ribs while still in the proximity of the umbilicus. The rapidly appearing bidichotomous or trivirgatitpartitous bundles arise in this fashion. Such bundles are already present at shell diameters of about 15 mm. Still later the primary ribs transform into typical bullae, at a diameter which depends on the *Polyptychites* species we are dealing with. This mode of development is completely absent in *Bodylevskites* species, including *B. pumilio*.

Genus *Paratollia* Casey 1973

Type species. *Paratollia kemperi* Casey 1973.

Diagnosis. Small Polyptychitinae with a slender and narrowly umbilicated shell. The primary ribs are very short and split up fast into the secondary ribs.

Discussion. The ammonites belonging to *Paratollia* belong to the least well known form groups, as only a few specimens of them have been found so far. Therefore, it is still impossible to pass a definitive judgment about the validity of the genus and its possible synonymy. Casey (1973, p. 257) provided the following definition of the generic characters: "Primitive Polyptychitinae resembling *Peregrinoceras* in discoidal shape and closeness of the costation, but with polyptychitine rib-bundling and pronounced bi-dichotomy in the adult. Suture-line ascending, *Polyptychites*-like." Like many other workers, Casey erroneously interpreted the trivirgatitpartitous bundles present in *Paratollia* as typical polyptychous rib bundles.

The genus comprises small species which are characterized by slender shells. The whorls are relatively high. Their flanks are only slightly convex while the venter is narrowly rounded. The successive whorls enclose the preceding whorls to a considerable degree and the umbilicus is moderately involute.

The suture line was so far studied only in *P. kemperi* Casey (Figure 13a). The adult external suture line of the holotype, which is clearly visible on the early half of the ultimate whorl, was correctly interpreted as "ascending, *Polyptychites* like" by Casey (1973, p. 257). The lobules of this only sparcely but moderately deeply denticulated suture line are characteristically rounded instead of acutely pointed. Already in the earliest visible sutures, the lobes of subsequent sutures touch (and locally overlap with) the tops of saddles of preceding sutures. The few oralmost sutures are pronouncedly approximated which results in a considerable overlap of most of their elements. The holotype is accordingly an adult. The first lateral lobe is only slightly shorter and smaller than the ventral lobe. These two lobes are separated by the first lateral saddle, which is about as wide as the ventral lobe. This saddle slightly narrows adorally and its forwardly-convex top is subdivided in two by a centrally situated, slender, feebly denticulated lobule.

The first lateral lobe is slender (about three times longer than wide), approximately parallel-sided and sparcely but moderately deeply denticulated. The long, finger-like shaped apical prongs are approximately symmetrically trifid.

The second lateral saddle is shaped and proportioned like the first, except that its forward-convex top is ornamented by two symmetrically placed, small, slightly notched lobules. It is either slightly narrower than or about as wide as the first lateral lobe.

The second lateral lobe is a slender, about four times longer than wide, distinctly adapically tapering structure, the length of which is about two-thirds that of the first lateral lobe. Its tip is pronouncedly asymmetrically trifid as one of the lateral prongs flanking the very slender and long central prong is situated considerably lower than the other. The lobules ornamenting its flanks are either simple or slightly notched.

The third lateral saddle, which occupies most of the lower third of the flank, is from one and a half to almost two times wider than the second lateral lobe. It expands somewhat adorally and its only slightly forward convex top is ornamented by three lobules. The central lobule is a relatively slender and long, adapically trifid and laterally slightly notched structure while the flanking lobules are tiny, round-tipped mounds.

The first auxiliary lobe is at first situated either on the umbilical shoulder or on the lowermost flank just before it. However, it becomes displaced farther on to the lowermost flank in the few oralmost sutures. It is a parallel-sided structure, which is about as slender as is the second lateral lobe (three to three and a half times longer than wide). The tip is symmetrically trifid with very short rounded prongs. Its flanks are ornamented by two pairs of simple, roundtopped, bulge-like lobules.

The fourth lateral saddle occupies at least the outer third of the umbilical wall and all of the umbilical shoulder on the earliest quarter of the ultimate whorl. However, neither its inner flank nor the second lateral lobe are visible on this strongly damaged part of the umbilical wall. At the oral end of the phragmocone, however, this saddle begins already on the lowermost (i.e. adumbilicalmost) part of the flank and extends across the umbilical shoulder onto the outermost umbilical wall only (Figure 13a). Here it is at least three times wider than the first auxiliary lobe and its straight umbilicalward ascendant top is ornamented by two tiny, apparently simple lobules.

The second auxiliary lobe was also seen only on the oralmost part of the phragmocone. It is a short and sturdy (only about one and a half times longer than wide), markedly adapically tapering, asymmetrically trifid structure, which is pronouncedly (at 25 to 30 degrees) inclined ventralward. It occupies about the middle half of the umbilical wall and is separated from the umbilical seam by what appears to be the outer two-thirds of the fifth lateral saddle. The forward convex top of this saddle is subdivided by a tiny, tack-like lobule which is situated within the inner third of its exposed part. No traces of the third auxiliary lobe was seen at the umbilical seam in the few sutures where the latter is visible.

The lateral part of the suture line, including the outer part of the third lateral saddle, is straight and ascends at about 30° in relation to the corresponding radius. Then it turns rapidly around until it becomes subradially oriented at the umbilical shoulder. Yet farther on the umbilical wall the suture line becomes distinctly descendant (5-?10°).

This external suture line of *Paratollia kemperi* resembles very closely that of *Peregrinoceras*? *albidum* (Casey, 1973, p. 255, Fig. 6h) in the pronouncedly ascendant orientation, shape, proportions and orientation of most of its lobes and saddles (except for the fourth lateral saddle and second lateral lobe) and the rounded instead of acutely pointed appearance of all lobules. However, the *P.*? *albidum* suture appears to be pronouncedly ascendant and straight all the way to and including the second auxiliary lobe. Furthermore, there appears to be space in this suture line for the third auxiliary lobe between the second auxiliary and the indicated umbilical seam. These two suture lines are deemed to be similar enough to indicate a close affinity of *Paratollia* and *Peregrinoceras* sensu Casey and they necessitate a transfer of the latter genus into the subfamily Polyptychitinae.

The suture line of *Paratollia* (and also that of *Peregrinoceras* sensu Casey?) resembles that of *Neocraspedites semilaevis* and other *Neocraspedites* in the pronouncedly ascendant orientation of its lateral part. However, it differs from that of *Neocraspedites* in every other respect, such as the orientation of its umbilical part, the absence of the third auxiliary lobe, entirely different shape and proportions of lobes and saddles and the rounded shape of the lobules.

The suture line of *Paratollia* differs even more strongly from the sutures of all other Polyptychitinae genera.

The sculpture is fine and dense, but its individual elements are high. The primary ribs are either not bullate or show only slightly bullae-like elevations. Their number per whorl is high in accordance with the density of the sculpture. The primary ribs split into secondary ribs very low on the flank, at least in the intermediate growth stages, instead of forming a longer stem. This splitting of primary ribs in the immediate proximity of the umbilicus provides a distinguishing feature from morphologically similar contemporary and older ammonites (e.g. *Peregrinoceras* sensu Casey, *Chandomirovia*, *Borealites*, etc.). Casey's indication of the presence of a pronounced bidichotomous ribbing habit in the adult is not valid for the English material of *Paratollia*. In the German material it is only valid for forms transitional to *Propolyptychites quadrifidus* (Koenen) and *Euryptychites diplotomus* (Koenen).

As *Paratollia* and *Peregrinoceras* sensu Casey have such similar sutures, they differ only in their rib bundling habit and in the number of primary ribs. *Paratollia* developed from *Peregrinoceras* sensu Casey via an increase in the number of primary ribs combined with the transference of their subdivision points into the proximity of the umbilicus. The two are connected by transitional forms, as Casey (1973, p. 257) established from the example of *Peregrinoceras*? *prostenomphaloides* (Neale). *Peregrinoceras*? sp. nov. cf. *albidum* Casey (1973, Pl. 10, fig. 3) is another example of such forms.

From *Bodylevskites Paratollia* differs first of all in an apparently complete absence of constrictions. The external suture lines of the two are similar in the presence of only two auxiliary lobes. However, they differ in the predominantly pronouncedly ascendant orientation of the *Paratollia* suture, the much greater slenderness of its lobes and the marked rounding of its lobules. Furthermore, *Paratollia* differs in the stiff and essentially straight appearance of its supplementary ribs and in a considerably lower (i.e. closely above the umbilical shoulder) branching point of its primary ribs.

The genus *Chandomirovia* Sazonov 1951, which resembles *Paratollia* in some morphological features, is most likely a homoeomorphic representative of the Craspeditidae.

The assignment of German representatives of *Paratollia* to the North Siberian genus *Neotollia* Shulgina 1969, which was tentatively proposed in the Soviet Union a few years ago (Shulgina in Saks et al., 1972, p. 99 and the table in the English translation of this paper), is not justified because of differences in the suture lines and sculpture of these only homoemorphic ammonites.

Paratollia is the rootstock of the genera *Propolyptychites* Kemper 1964, *Euryptychites* Pavlow 1914 and *Neocraspedites* Spath 1924. This conclusion is supported by the existence of morphologically transitional forms between *Paratollia* on the one hand and the genera *Propolyptychites* and *Euryptychites* on the other (e.g. *P. tenuicostata* Kemper described below).

It is remarkable that these evolutionary changes parallel closely the transformation of North Siberian representatives of *Bodylevskites* into *Siberiptychites* s. str. and *Astieriptychites*.

Paratollia kemperi Casey 1973

Pl. 7, fig. 6; Pl. 26, figs. 3A, 3B; Figure 13a.

Synonymy

1964 *Tollia tolmatschowi* Kemper, p. 21, Pl. 1, figs. 3a, 3b.
1968 *Tollia tolmatschowi* Kemper, Pl. 22, fig. 6.
*1973 *Paratollia kemperi* Casey, p. 257, Pl. 5, figs. 5a, 5b; figs. 6j-6k.
1976 *Paratollia kemperi* Kemper, p. 34, Pl. 22, fig. 6.

Holotype. The specimen reproduced by Kemper (1964, Pl. 1, fig. 3a, 3b; this paper, Pl. 7, fig. 6; Figure 13a) by original designation (Casey, 1973, p. 257), BGR, Hannover, Cat. No. kv 341.

Locus typicus. Suddendorf.

Stratum typicum. Lower lower Valanginian, upper *Platylenticeras*-Beds.

Material. The holotype from Suddendorf and a poorly preserved, smaller specimen from Jetenburg-Bueckeburg (BGR, kv 351).

Diagnosis. Small species with slender and high whorls, which are higher than wide. The venter is narrowly-arched and the umbilicus narrow. The sculpture is fine and dense. The bundling habit has a predominantly trivirgatitpartitous character.

Measurements (in mm).

Specimen	Shell diameter	Width of Umbilicus	wh 1	wh 2	wth 1	wth 2
Holotype. BGR. kv 341	47	10(21)	15.5(32)	21(45)	13?	—

(The above values are not entirely reliable because of a deformed state of the holotype)

Description. The holotype is evidently adult. It retains a half whorl of the living chamber, which is however somewhat deformed laterally. In spite of that, there is no doubt that this shell is very slender. The diameter of the adult shell may be estimated at 65 mm.

The whorls are higher than wide. The flanks are only moderately convex and connected by a narrowly arched, rounded venter. Addorsally the flanks merge into a low but steeply inclined umbilical wall across a broadly-rounded umbilical shoulder. The narrow umbilicus is accordingly shallow and step-like rather than funnel-like.

The suture line was described in the descriptiion of the genus (see Figure 13a).

The sculpture is very fine and dense but its individual elements are high. The primary ribs are short and pronounced but not bullate. The last preserved half whorl has about 14 primary ribs. Their total number on the last whorl cannot be counted exactly but is estimated to be 28 to 30. The primary ribs split up into the secondary ribs close to the umbilicus.

The last preserved whorl is ornamented by trivirgatitpartitous rib bundles, which alternate with intercalated single ribs and also with intercalated dichotomous ribs. These intercalated ribs are not connected with the primary ribs. They may, at the most, touch the anterior secondary ribs. The remarkable density of the sculpture is, therefore, not caused by an increased number of ribs in individual bundles (as happens in *Prodichotomites* species) but by a dense sequence of primitive polyptychitine bundles associated with some intercalated ribs. There is no tendency for a weakening of the sculpture on the flanks. The second German specimen (BGR, kv 351) shows that the trivirgatitpartitous bundles are yet more markedly developed on the earlier whorls.

The species is so far known only from Northwest Germany, but related forms occur at Speeton.

Affinities and differences. *P. kemperi* may be interpreted as the morphologically extreme member of the *Paratollia*-lineage. It differs from other representatives of the genus in its smaller size and the particularly slender proportions of the shell. From *P. tenuicostata* it differs also in its trivirgatitpartitous bundling habit.

Paratollia cf. *kemperi* Casey 1973

Discussion. Casey (1973, Pl. 5, fig. 5a, 5b) figured a small ammonite from the Claxby Beds as *Paratollia* cf. *kemperi*. This specimen combines slender whorl proportions with a fine and dense sculpture. However, the sculpture at the beginning of the last whorl resembles still that of *Peregrinoceras* sensu Casey 1973 because of the length of primary ribs and the adventral positioning of their branching points. It is, therefore, possible to interpret this specimen as representing a form closely allied to the root of the *Paratollia* lineage.

Paratollia emslandensis (Kemper 1964)

Pl. 1, fig. 5

*1964	*Polyptychites (Propolyptychites) emslandensis* Kemper, p. 24, Pl. 1, fig. 1a, 1b; Pl. 2, fig. 5.
1968	*Polyptychites (Propolyptychites) emslandensis* Kemper, Pl. 12, figs. 1a, 1b.
1976	*Polyptychites (Propolyptychites) emslandensis* Kemper, p. 34, Pl. 12, figs. 1a, 1b.

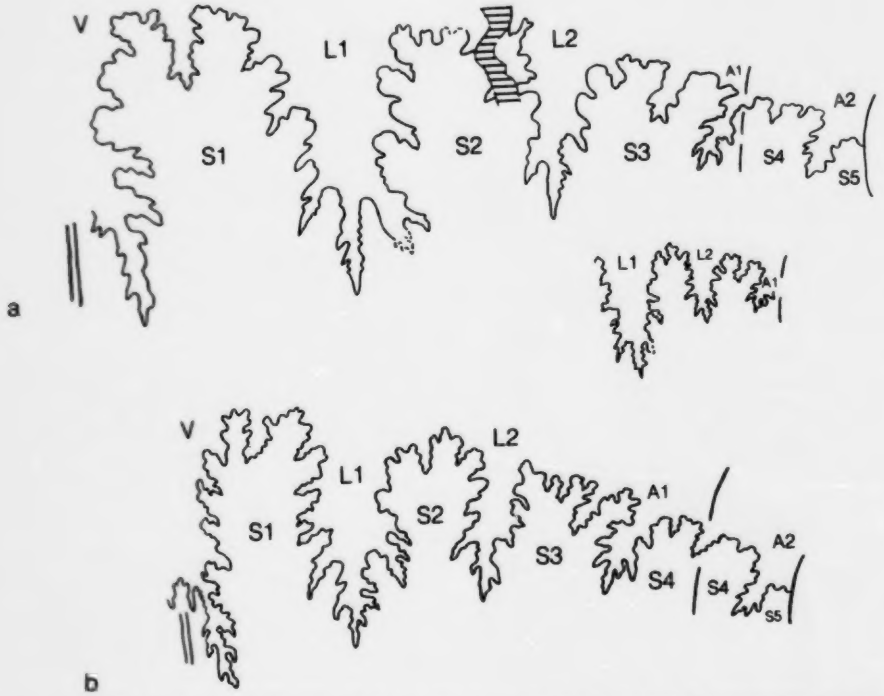


Figure 13. Adult external suture lines of *Paratollia kemperi* Casey, 1973 and *Neocraspedites semilaevis* (Koenen, 1902). **a**. Two advanced adult sutures of the holotype of *P. kemperi* reproduced in Pl. 7, fig. 6 (see there for the locality data). The complete suture line occurs on the early part of the adult ultimate whorl at the whorl height (wh) of about 19 mm, x 6.5 (approximate). The partial suture (lobes L1 to A1 only) occurs on the oralmost part of adult penultimate whorl at the whorl height (wh) of about 15 mm, x 6.5 (approximately). **b**. *Neocraspedites semilaevis* (Koenen, 1902). Unnumbered and otherwise unfigured example from Sachsenhagen, Northwest Germany, preserved in the University of Goettingen collection. A morphologically aberrant (two auxiliaries only; see p. 38 for further details) external suture exposed on the adult penultimate whorl at the whorl height (wh) of about 25 mm, x 6.4 (approximate).

Holotype. The specimen figured by Kemper (1964, Pl. 1, figs. 1a, 1b; Pl. 2, fig. 5) is the holotype of *Paratollia emslandensis* by original designation, BGR, Hannover, kv 342.

Locus typicus. Suddendorf.

Stratum typicum. Upper *Platylenticeras*-Beds, lower lower Valanginian.

Material. The solitary holotype.

Diagnosis. A small species. The whorls are only moderately slender, always wider than high and with an obtusely rounded venter. The flanks are only feebly convex. The sculpture is dense. Ribs are very high and predominantly trivirgatitpartitous.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
Holotype, BGR, kv 342	—	—	21	27	23	31

Description. The solitary holotype is deformed in the dorso-ventral direction. Therefore it was impossible to obtain exact values of the shell diameter and the width of the umbilicus. However, its umbilicus was apparently narrow. The suture line is not visible so that it is uncertain whether or not the whole of the last whorl is a living chamber. However, the character of the sculpture suggests that this whorl represents an adult living chamber. The last whorl is always wider than high (see the table of measurements). The narrow arch of the venter is slightly flattened. The flanks are only slightly convex and converge toward the venter. They merge into a low and relatively gently inclined umbilical wall across a broadly rounded umbilical shoulder.

The sculpture is dense and fine, but its individual elements are extraordinarily high and actually sharp-topped. The primary ribs are unusually short, limited to the umbilical shoulder and feebly bullate at the beginning of the last whorl. Thereafter they expand gradually in the dorso-ventral direction to the end of the whorl, rapidly losing their slightly bullate appearance.

The earliest visible rib bundle consists of a trivirgatitpartitous posterior element and a dichotomous anterior element. These two elements originate directly from the bulla. The following bundles are trivirgatitpartitous. However, additional dichotomous ribs continue to occur occasionally. These ribs are either intercalated between the bundles or are connected with the primary ribs. The latter condition results in a recurrence of the above described more complicated rib bundle.

The species is known only from Northwest Germany, but closely allied forms occur in the Speeton Clay.

Affinities and differences. *P. emslandensis* is a larger and thicker form than *P. kemperi* and has a broader, lower ventered whorl section. It is smaller and more slender than *P. tenuicostata*, from which it differs additionally in a trivirgatitpartitous mode of bundling.

Paratollia aff. *emslandensis* (Kemper 1964)

1973 *Propolyptychites* sp. Casey, Pl. 5, fig. 6.

Discussion. The small ammonite figured by Casey (1973, Pl. 5, fig. 6) from the *Paratollia*-level of the Claxby Beds has an umbilicus that is wide for a *Paratollia*. Furthermore, its whorls are low for representatives of that genus. This specimen is ornamented exclusively by trivirgatitpartitous rib bundles consisting of high and strongly developed ribs. It could well be a predecessor of *P. emslandensis* (Kemper).

Casey's (1973) proposal to place this specimen in *Propolyptychites* is contradicted by its trivirgatitpartitous ribbing habit. This habit is either absent in *Propolyptychites* or, at the very most, is restricted to an early growth stage.

Paratollia tenuicostata (Kemper 1968)

Pl. 1, figs. 3, 4

1964	Transitional form between *Polyptychites (Propolyptychites) emslandensis* and *P. (Propolyptychites) quadrifidus* Kemper, p. 24, Pl. 2, figs. 6a, 6b.
*1968	*Polyptychites (Propolyptychites) tenuicostatus* Kemper, Pl. 23, fig. 12.
1976	*Polyptychites (Propolyptychites) tenuicostatus* Kemper, p. 34, 172, Pl. 23, fig. 12.

Holotype. Specimen figured by Kemper (1976, Pl. 23, fig. 12) is the holotype of *Paratollia tenuicostata* by original designation. BGR, Hannover, kv 58.

Locus typicus. Suddendorf.

Stratum typicum. Upper *Platylenticeras*-Beds, lower lower Valanginian.

Material. 4 specimens from Suddendorf.

Diagnosis. A large species for the genus with narrow umbilicus and rather thick whorls (width greater than height). Sculpture is dense and fine. The ribs are high and form predominantly bidichotomous bundles, at least in the intermediate and adult growth stages.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
Holotype, BGR, kv 58	73	18(25)	24(33)	32(44)	29?	37
Specimen from Hendriksen coll.	71	18(25)	23(32)	29(41)	—	—

Description. The last whorl of the holotype is occupied almost entirely by the living chamber. However, it is uncertain whether or not the specimen is an adult. The last whorl is moderately thick. Its maximum width is situated in the area of the umbilical shoulder. The last whorl is distinctly wider than high at first but by the end of the whorl the height becomes almost equal to the width. The flanks are but slightly convex and they are joined by a relatively narrow rounded venter. The successive whorls enclose the preceding whorls very strongly (about 86%). The umbilical shoulder is pronouncedly rounded and the umbilical wall moderately high and (at 75 to 80° in relation to the plane of symmetry) moderately steep. The narrow umbilicus (25%) has a funnel-like shape. The external suture was not observable in its entirety but is most likely of a polyptychitinid type.

The sculpture consists of 22 short primary ribs, which continue onto the umbilical wall as comma-like bent, forwardly concave extensions. The secondary ribs rapidly (i.e. low on the flank) split off the primaries: they are attenuated but nevertheless high and sharp. In the intermediate growth stages the bundling follows the bidichotomous style, but the points of subdivision do not occur at exactly the same height. On the last whorl the ribbing habit becomes more irregular because of intercalation of solitary or dichotomously forked secondary ribs. Furthermore, on this whorl, a single additional secondary rib may be inserted between both forks of the bundle. There is no *Neocraspedites*-like weakening of the sculpture on the flanks.

The specimen from the Hendriksen (Almelo) collection figured by Kemper (1964, Pl. 2, fig. 6a, b) and reproduced herein in Pl. 1, fig. 4 is a somewhat more coarsely ribbed and thicker-whorled variant of *Paratollia tenuicostata*. The primary ribs of this specimen are somewhat bullate. Yet another specimen has higher whorls and a still more narrow umbilicus. The ribbing habit is more irregular and differs also in a very adventral subdivision of secondaries into tertiary ribs.

Affinities and differences. The species comprises the relatively larger and thicker representatives of the genus. These features, and also the bidichotomous ribbing habit, distinguish *Paratollia tenuicostata* from other *Paratollia* species. The latter are smaller, more slender forms, which are characterized by a largely trivirgatitpartitous ribbing habit.

Genus *Euryptychites* Pavlow 1914

Type species. *Olcostephanus latissimus* Neumayr and Uhlig 1881.

Pavlow (1914, p. 36) erected the new subgenus *Euryptychites* for (Jeletzky's translation from Russian): "*Polyptychites* of the group of *Polyptychites (Euryptychites) latissimus* Neum. et Uhl." This indication falls short of a formal designation of *Olcostephanus latissimus* Neumayr et Uhlig 1881 as the type species of *Euryptychites*. However, this species was unanimously recognized as such by subsequent workers until the selection was formally made by Wright in the Ammonoidea Volume of the Treatise (Wright *in* Arkell, 1957, p. L348). The subsequent designation of *Polyptychites gravesiformis* Pavlow 1892 by Voronets (1962, p. 78) is invalid.

Diagnosis. Polyptychitinids characterized by *Cadoceras*-like shape and proportions of all growth stages with the shell diameter exceeding 10 mm. The adult external suture has, as a rule, only two auxiliary lobes. Constrictions are absent.

Discussion. *Euryptychites* was originally defined by Pavlow (1914, p. 36) as follows (Jeletzky's translation from Russian): "I designate as *Euryptychites* that group of polyptychitids which differs from others in its strongly expanded or barrel-like shape, caused by a strong development of the siphonal side. This is combined with such contraction of the flanks that they only form the umbonal margin (i.e. umbonal shoulder) which connects the siphonal side with the umbonal side. The surface of the latter is also strongly expressed forming a deep umbilicus.

"In typical representatives the suture line is characterized by long and narrow saddles, three of which are situated on the siphonal side. Of these saddles two lateral ones are situated farther forward (i.e. oralward) in comparison with the outer saddle. The typical representatives of this subgenus, *Polyptychites gravesiformis* Pavl., *P. praelatus* Koen., *P. diplotomus* Koen., *P. globulosus* Koen., *P. scalarinus* Koen., *P. latissimus* Neum. et Uhl. also approach such typical forms[1], except for the somewhat less elongated saddles. In addition to these typical *Euryptychites*, there is another series of forms which combine more or less expanded and barrel-shaped whorls with relatively considerably shorter and wider saddles and lobes. They appear to form another lineage parallel to *Euryptychites*. This lineage begins already in the Jurassic with such forms as *Ammonites gigas* d'Orb. (non Zieten), *A. gravesi*, *A. irius*. In the Neocomian this lineage includes *P. bullatus* Koen., *P. nucleus* Roem., *P. marginatus* (Phil.) Neum. et Uhl., *P. infundibulum* Koen., *P. sphaeroidalis* Koen., *P. acuticosta* Koen."

Hence *Euryptychites* Pavlow 1914, which was proposed as a subgenus of *Polyptychites*, was erected for a great variety of forms characterized by a combination of wide whorls with almost globular shell shape.

The largest species have whorl diameters up to 230 mm (Sachsenhagen) and so are as large as a human head. They are among the largest Polyptychitinae in Northwest Germany.

The cadicone genus or subgenus *Euryptychites*, the rank of which remains disputable, is the least understood group of Valanginian ammonites. It is so far impossible to interpret it definitively, for several reasons. The most important is an insufficient understanding of the temporal sequence of its species and of their ontogenetic development. Another reason is that several other not directly related, polyptychitinid species may develop quasi-cadicone adult whorls.

Although it cannot be conclusively demonstrated as yet, it appears likely that the *Euryptychites*-shaped species in Northwest Germany are confined to two different levels. One is the *Platylenticeras*-Beds and lowermost

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[1] Like the original Russian text, this translation is ambiguous. There are no other typical species, except for those named herein.

Polyptychites Beds of the lower Valanginian while the other is the boundary beds of the lower and upper Valanginian. Only the thickened extreme forms of *Polyptychites*-species, which cannot be assigned to *Euryptychites*, occur in the intervening beds. According to this interpretation, which agrees with the above cited suggestion of Pavlow (1914, p. 36), these truly cadicone ammonites from the Valanginian of Northwest Germany form two independent, homoeomorphic offshoots of the Polyptychitinae. The name *Euryptychites* could only be used validly for one of these two lineages, namely that which contains the designated type species, *"Olcostephanus"* *latissimus* Neumayr and Uhlig. Its holotype, from Osterwald, is in the Roemer-Museum in Hildesheim. It is not known at which level it was found. However, it is probably from the *Platylenticeras*-Beds (lower part of the lower Valanginian). If so, the name *Euryptychites* is valid for the early Valanginian cadicone species alone. The recognition of *Euryptychites* depends on the growth stage at which the *Cadoceras*-like whorls begin. In the true *Euryptychites* the very early growth stages with the shell diameters less than 1 cm are already cadicones (Pl. 3, fig. 2; Kemper, 1976, Pl. 1, fig. 3). Such forms are eucadicone shells.

The study of more slender variants of *E. diplotomus*, which is the ancestral group of *Euryptychites*, suggests a gradual extension of the cadicone cross-section from the more advanced growth stages into ever earlier growth stages. If so, *Euryptychites* is characterized by a palingenetic rather than by a proterogenetic development. In the case of a palingenetic ontogenetic mode a diagnostic delimitation of *Euryptychites* from *Polyptychites* or *Propolyptychites* could only be achieved by assigning an arbitrary diagnostic size at which the cadicone shape of the whorl's cross-section begins in each of these genera.

It is not possible to make a definitive generic assignment of those *Euryptychites*-like species, which are based solely on the descriptions of living chambers. They are, in part, the extreme variants of other species, which become *Cadoceras*-like (pseudo- or quasi-cadicones) only in advanced growth stages. A good example of such quasi-cadicone whorl shape restricted to the advanced whorls alone is provided by *Polyptychites sphaeroidalis-hapkei* group here (Pl. 9, fig. 4C). Other such forms, which are most likely extreme morphological variants of the variable *keyserlingi* species group, are:

P. acuticosta Koenen 1909 (Pl. XII, figs. 1, 4)
P. arcuatus Koenen 1909 (Pl. XI, figs. 2, 4)
P. costellatus Koenen 1909 (Pl. IX, figs. 1, 2)
P. infundibulum Koenen 1909 (Pl. III, figs. 1, 2) and
P. robustus Koenen 1909 (Pl. III, figs. 3, 4)

The same appears to be true of *P. subgravesi* Spath 1924 and *P. pyritosus* Spath 1924, which were originally figured by Pavlow (in Pavlow and Lamplugh, 1892). Yet another example is provided by the quasi-cadicone high Boreal *Pseudoeuryptychites* Jeletzky 1986 described later in this paper.

All of the above mentioned, figured specimens from Northwest Europe exhibit a basically polyptychitinid sculpture with clearly expressed senile features. Furthermore, they have only a small number of high and large bullae. The true *Euryptychites* species posses, in contrast, a considerably greater number of finer bullae. These bullae, as a rule, extend much farther forward on the umbilical wall. They also sit on the generally acute umbilical shoulder, which represents in this genus a true acute rim.

Only *"Euryptychites"*? *marginatus* Roemer (non Phillips?), which is anyway very problematic in its true affinities, represents an exception where the shape and the number of bullae are concerned. It is extremely questionable whether or not that name, proposed by Phillips (1829) for a juvenile form, can be applied to the large specimen from Osterwald as Neumayr and Uhlig (1881) did. According to Rawson (1971), the juvenile form of Phillips is a species of *Simbirskites*. No other specimens comparable with the large and poorly figured specimen from Osterwald have been found in the Valanginian of Northwest Germany. Therefore, one can doubt whether or not this specimen was really found in the Valanginian. Perhaps it is a misplaced Jurassic ammonite.

The early early Valanginian species *E. diplotomus* (Koenen 1902), which represents a still pronouncedly polyptychitoid ancestral group, and the more progressive *E. latissimus* (Neumayr and Uhlig, 1881) are undoubtedly true *Euryptychites*. *E. traillensis* Donovan 1953 and *E. laevis* Donovan 1953 from Greenland are evidently of the same age and affinities as these early species from Germany.

The auxiliary parts of all presently known external suture lines of *Euryptychites* are suspensive in relation to their lateral parts. Another distinctive feature is the prevalence of only two lateral lobes on the ventral surface (i.e. ventral and lateral sides combined). This is almost invariably combined with the presence of only two auxiliary lobes on the umbilical side. This is true of the type species as well as of *E. traillensis* and *E. laevis* (see Donovan 1953, Pl. 22, fig. 1e; Text-fig. 9). It also applies to *E. gravesiformis* (see Pavlow in Pavlow and Lamplugh 1892, Pl. XIII, fig. 7c; Text-fig. on p. 483; Pl. VIII, fig. 14c), which the writers place in *E. latissimus* (see p. 33). The first auxiliary lobe may be situated on the umbilical shoulder in some representatives of *E. diplotomus* (Figure 16b). However, such specimens still have only two auxiliary lobes. A well defined third auxiliary lobe is unknown in *Euryptychites*. A small adumbilicalmost element that can be tenuously interpreted as an incipient or ill delimited third auxiliary lobe was observed very rarely in *E. diplotomus* (e.g. in BGR, kv 332; Figure 16a) and *E. latissimus* (e.g. in BGR, kv 334; Figure 14a).

The appearance of lateral lobes is rather variable. One morphological extreme is exemplified by *E. latissimus* (Neumayr and Uhlig, 1881, Pl. XXVIII, fig. 1b and personal observations) where these lobes are extremely slender and long, parallel-sided (the adapically tapering shape of the first lateral lobe in this drawing is an artist's error) and very deeply and elaborately denticulated. The other morphological extreme is provided by *E. traillensis* and *E. laevis* (Donovan, 1953, Pl. 22, fig. 1e, 3a; Text-fig. 9) where these lobes are pronouncedly to extremely widened, relatively to very short, and taper distinctly to pronouncedly adapically. It is not certain whether the relatively simple, shallowly denticulated suture lines of these East Greenland species are primitive or secondarily simplified.

The relatively simple external suture line of the true *Euryptychites gravesiformis* Pavlow 1892 (in Pavlow and Lamplugh; 1892, Pl. XIII, fig. 7c, Text-fig. on p. 483) appears to be transitional between these two extremes.

The external suture lines of *E. latissimus* and *E. gravesiformis* s. str. resemble closely that of *Propolyptychites quadrifidus* (Koenen) (1902, Pl. III, fig. 10) and those suture lines of *Euryptychites diplotomus* Koenen (1902, Pl. LIV, fig. 3a, 3b) which have only two lateral lobes on the flank. This supports the idea of derivation of *Euryptychites* s. str. from *Propolyptychites* ex gr. *quadrifidus* via its most primitive species *E. diplotomus* (Koenen). At the same time these suture lines differ markedly from the external sutures of those North Siberian and Canadian representatives of *Siberiptychites* which have developed an *Euryptychites*-like shell (e.g. "*Euryptychites gravesiformis*" of Pavlow (1914) or *Siberiptychites (Pseudoeuryptychites) pavlovi* Voronets 1962). These cadicone species are also characterized by the presence of only two lateral lobes on their siphonal side. However, they differ in the presence of at least three auxiliaries on their umbilical wall and by a relatively greater width of their saddles which are always considerably to much wider than the preceding lobes (which are also relatively more narrow than their equivalents in true *Euryptychites*; Voronets, 1962, Figures 29-31). These *Cadoceras*-like representatives of *Siberiptychites* also differ from true *Euryptychites* in a constant presence of constrictions, which were never observed in the latter genus, and a considerably later appearance of truly cadicone whorl shape and proportions (see *Pseudoeuryptychites* for further details). Because of the scarcity of the material available and the unresolved problems discussed above, it is difficult to provide a detailed and definitive description of *Euryptychites* yet. The following account is, therefore, limited to the description of the following, most important species: *E. latissimus*, the type species of the genus, *E. diplotomus*, its rootstock, and *E.* aff. *laevis*, a connecting link to its East Greenland representatives.

The younger species group of cadicone Polyptychitinae, typified by "*Polyptychites*" *sphaericus* Koenen 1902, is interpreted here as an independent offshoot of the subfamily. This species group is excluded from *Euryptychites* and described below as *Hollwediceras* n. gen.

It is still impossible to evaluate "*Polyptychites*" *juillerati* Baumberger 1908. This species resembles the true *Euryptychites* of the early Valanginian in its coarse ribbing habit, the small number of ribs in a bundle and the trivirgatitpartitous bundling habit. However, it is supposed to be derived from the *Astieria*-marls (Baumberger, 1908) and so should be considerably younger than the true *Euryptychites* forms.

As will be demonstrated below, a number of Arctic cadicone polyptychitinids described and figured as *Euryptychites* in the Russian literature *(e.g.* "*Euryptychites*" *gravesiformis* Pavlow 1914 non 1892, "*E.*" *pateraeformis* Voronets 1962 and "*P.*" *pavlowi* Voronets 1962) are merely homoemorphic derivatives of the *Siberiptychites* lineage. They are described below as a subgenus *(Pseudoeuryptychites)* of *Siberiptychites*. However, the evaluation of some other cadicone representatives of Polyptychitinae described from the Arctic basins remains difficult. The genus *Euryptychites* s. str. is so far only known definitely from Northwest Europe, Central Russia and East Greenland.

Euryptychites latissimus (Neumayr and Uhlig 1881)

Pl. 3, fig. 2A, B; Pl. 26, fig. 1, 4; Pl. 27, fig. 1, 4; Figures 14a-14c.

*1881 *Olcostephanus latissimus* Neumayr and Uhlig, p. 158, Pl. XXVIII, fig. 1a, 1b.

1892 *Olcostephanus (Polyptychites) gravesiformis* Pavlow, in Pavlow and Lamplugh, p. 482-484, Pl. 8, fig. 14a-c; Pl. 13, figs. 7, 8, Text-fig. on p. 483.

1902 *Polyptychites bullatus* Koenen p. 138-140, Pl. 55, fig. 3; non 1902 *Polyptychites latissimus* Koenen, p. 129, Pl. 54, fig. 1a, b and Pl. 55, figs. 6a, 6b, 12a, 12b.

1957 *Polyptychites (Euryptychites) latissimus* Wright in Arkell et al., p. 348, fig. 456-3a, 3b.

1976 *Polyptychites (Euryptychites)* juv. sp. Kemper, Pl. 1, fig. 3.

Holotype. The original of Neumayr and Uhlig (1881, Pl. XXVIII, fig. 1a, 1b) by monotypy. The original is in Roemer-Museum, Hildesheim. Plaster cast in BGR, Hannover, kv 62.

Locus typicus. Osterwald. Federal Republic of Germany.

Stratum typicum. Uncertain. Presumably *Platylenticeras*-Beds of the lower lower Valanginian.

Material. 9 specimens.

Diagnosis. Large typically cadicone ammonites with a relatively wide, funnel-like umbilicus; bullae appear early and are typically expressed; most rib bundles include 3 to 4 supplementary (i.e. secondary and tertiary) ribs, of which three secondaries originate directly in the bulla with the posterior secondary bifurcating fairly high on the flank; this results in a predominantly quadrifasciculate bundling habit; the trivirgatitpartitous bundling habit may also be present but the bidichotomous habit is totally unknown.

Measurements (in mm).

Specimen	Shell Diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
Holotype	115	41(36)	33(39)	41(36)	68?	—
BGR, kv 371	72	25(35)	21(29)	26(36)	—	—
BGR, kv 369	58	17(29)	18(31)	23(40)	32?	45
BGR, kv 334	126	44(35)	34(27)	49(39)	86	112

Discussion. In the holotype one can only observe the solitary whorl figured by Neumayr and Uhlig (loc. cit.). The drawing is not entirely correct. However, it provides a satisfactory reproduction of the recognizable pecularities of the original. Koenen's (1902, Pl. 54, fig. 1a, 1b; Pl. 55, figs. 6a, 6b, and 12a, 12b) placement of some juvenile ammonites into this species cannot be substantiated and is most likely erroneous.

The holotype is chambered to the end, which precludes any conclusions about the size reached by the species. The whorl available is low and low-arched. Its umbilical shoulder is relatively sharp-angular and forms an edge in the truest sense of this word. The umbilical shoulder is ornamented by about 25 slightly elevated bullae. These bullae are inclined forward on the rather strongly oblique umbilical shoulder and are expressed there as obliquely directed prominent welts. These welts are either equally strongly or more strongly expressed than the ribs in the proximity of the umbilical shoulder.

At the beginning of the last preserved whorl the rib bundles consist of three supplementary ribs; a solitary anterior rib and a dichotomous posterior rib. On the oral half of this whorl the number of supplementary ribs per bundle is increased by the addition of one intercalated secondary. On the last quarter, finally, the division point of the posterior dichotomous element migrates toward the bulla in such a fashion as to produce an approximately fasciculate bundle consisting of four secondaries. The secondaries are not radially oriented but form forwardly convex arches.

Several specimens from Jetenburg show the morphology of intermediate growth stages. As one can see in the juvenile specimen BGR, kv 72 reproduced in Pl. 3, fig. 2, the whorls are cadicone already in the early juvenile growth stage (at least by a shell diameter of 0.7 mm; estim). The umbilical shoulder and the umbilical wall form a continuous broadly convex surface in this growth stage. Most of the specimens retain these whorl proportions also in the later ontogenetic stages. This results in a deep and funnel-like appearance of the umbilicus. Only a few specimens exhibit a gradual steepening of the umbilical wall coupled with a sharpening of the umbilical shoulder.

The bullate primary ribs are present already at a whorl diameter of 10 mm where they number 17 to 20 per whorl. They give rise to fasciculated rib bundles, which consist of 3 to 4 supplementary ribs. Beginning with a whorl diameter of about 15 mm the bundles consist of 4 supplementary ribs. The bundles consisting of an anterior solitary rib and a posterior trivirgatitpartitous element are rare. For the most part two solitary secondaries branch from a frontal part of the bulla and a bifurcating secondary element branches off behind them. As the subdivision point of the posterior bifurcating element may be situated rather addorsally, the bundle acquires an approximately fasciculate appearance. Such bundles represent a normal bundling habit at shell diameters approaching 60 mm (e.g. BGR, kv 370). However, there are variants with more (e.g. BGR, kv 369) and less (BGR, kv 371) ribs per bundle. Specimen BGR, kv 371 has also 4 supplementary ribs per bundle until a whorl diameter of about 50 mm. However, their number is somewhat reduced thereafter so that it acquires a predominantly trivirgatitpartitous ribbing habit. It has 22 bullae per whorl. This specimen probably represents only an extreme of the intraspecific variability and does not belong to a separate species. This variant differs from the Greenland species *E. traillensis*, which is also characterized by trivirgatitpartitous bundles, in a coarser sculpture, lesser number of bullae and a funnel-like umbilicus.

In the densely ribbed variant (BGR, kv 369) 3 solitary secondaries and a posterior bifurcating secondary branch off each bullae. The bullae are pronounced in spite of the delicate character of the ribbing. This variant has only 13 to 14 bullae per whorl, which is a remarkably small number for the species. Possibly if more material of this form were available it would be necessary to segregate it into a separate species. This action may find further support in the width of the umbilicus of our form, which is less than that of other representatives of *E. latissimus*.

An exceptionally well preserved *Euryptychites* from Sachsenhagen (BGR, kv 334) agrees well with the appearance of *E. latissimus* where its wide and low whorls are concerned. However, it has only 17 bullae on its last whorl which is an adult living chamber in part. It would appear that such sculptural differences reflect age differences within *E. latissimus* as its considerably smaller holotype is septate to the end. The Sachsenhagen specimen has an adult shell diameter of about 170 mm. This specimen and the others figured herein indicate also the early early Valanginian age of *E. latissimus* and other morphologically similar ammonites.

As already recognized by Neumayr and Uhlig (1881, p. 158, Pl. 28, fig. 1b), the external suture line of *Euryptychites latissimus* is characterized by a considerable slenderness of the stems of its lobes. This attenuation of lobes is coupled with a corresponding widening of the saddles contrary to the conclusion of the above workers.

The study of the external suture line on the plaster cast of the holotype indicates that its lateral lobes are 5 to 6 times longer than their stems are wide and very deeply and complexly denticulated. The stem of the first lateral lobe slightly tapers adapically to its asymmetrically trifid apex. That of the second lateral lobe is parallel-sided to its almost symmetrically trifid terminal prongs. The first lateral lobe is about as long as the similarly richly and deeply indented ventral lobe. The length of the second lateral lobe comprises about three-quarters that of the first lateral lobe and its width is somewhat less than one-half that of the first lateral.

Both lateral saddles are unusually wide in relation to the width of flanking lobes. The first lateral saddle is about twice as wide as the ventral lobe and about three times wider than the first lateral lobe and about 3 times wider than the first auxiliary lobe while the second lateral saddle is 6 to 6 1/2 times wider than the second lateral lobe and about 3 times wider than the first auxiliary lobe. The pronouncedly forward convex top of the first lateral

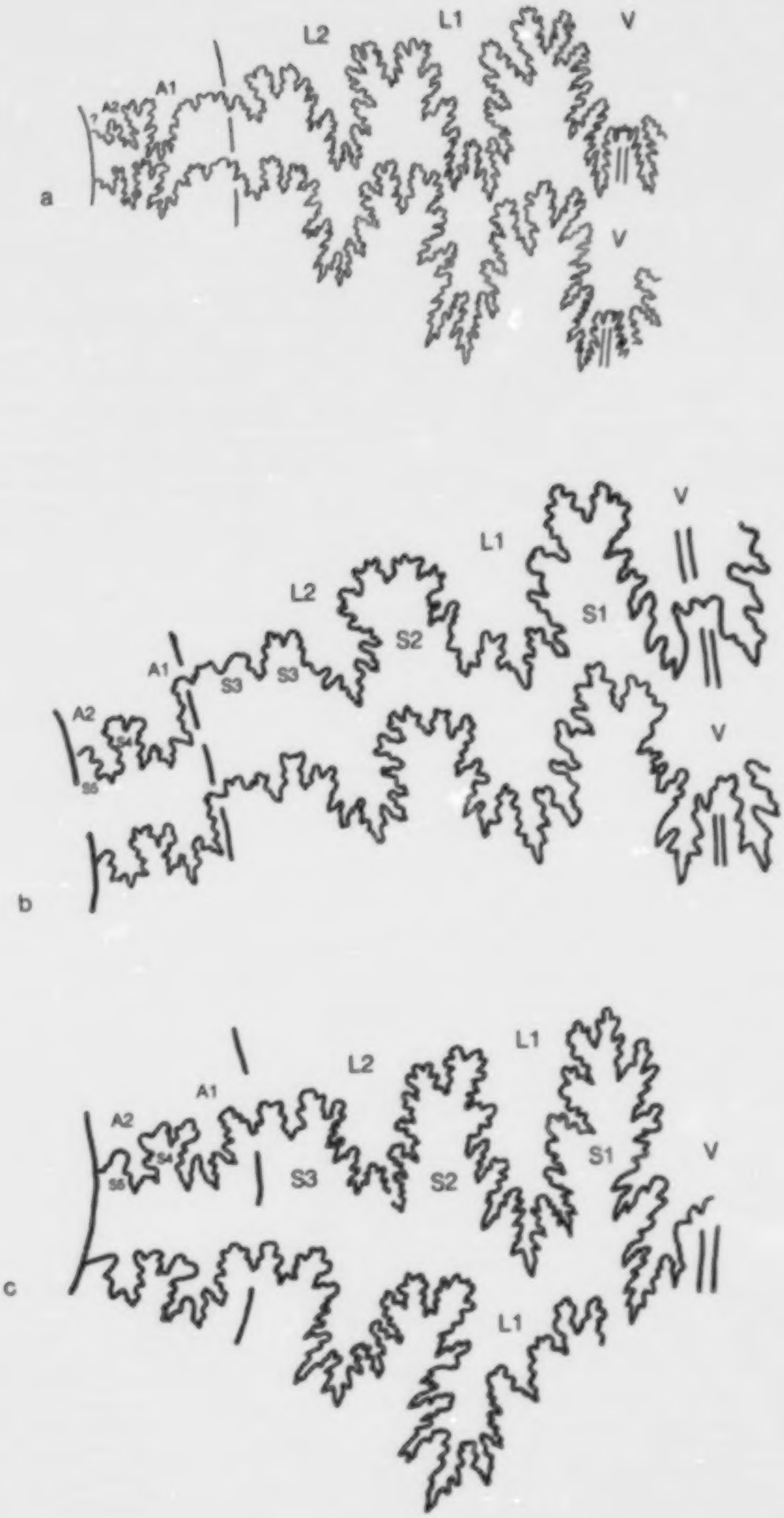

Figure 14. Adult external suture lines of *Euryptychites latissimus* (Neumayr and Uhlig, 1881). **a.** Specimen BGR, kv 334 from Sachsenhagen, Northwest Germany. Lower *Polyptychites* Beds, early early Valanginian. A complete advanced adult suture line visible on the adult penultimate whorl at the whorl height (wh) of about 100 mm, x 2. The suture is aberrant in exhibiting what may be an underdeveloped third auxiliary lobe marked with a question mark. **b.** Specimen BGR, kv 370 from Bueckeburg-Jetenburg, Northwest Germany. *Polyptychites*-Beds, early Valanginian. Early adult suture visible at the whorl height (wh) of about 23 mm, x 2 (approx.). **c.** Specimen BGR, kv 369 from the Bueckeburg-Jetenburg, Northwest Germany. *Polyptychites*-beds, early Valanginian. Early adult suture visible at the whorl height (wh) of about 23 mm, x 2 (approx.).

saddle is subdivided by no less than four slender deeply denticulated lobules. The two largest of these are marginally situated while the smallest is centrally situated.

The pronouncedly forward convex top of the second lateral saddle is subdivided by three lobules, which resemble those of the first lateral saddle in their size, proportions and denticulation. The third lateral saddle is about one and a half times wider than the second, it occupies the lowermost part of the flank, all of the angular umbilical shoulder and the outermost third of the umbilical wall. The somewhat poorly exposed, approximately straight, subtransversally oriented top of this saddle is subdivided by at least four first order lobules. The adventralmost lobule is a tiny and slender but relatively short, only slightly denticulated structure. The second lobule, which occurs just short of the umbilical shoulder, is similarly shaped and denticulated but at least three times wider and somewhat longer. The remaining two lobules, which are situated on the outermost part of the umbilical wall, are tiny, tack-like shaped, only slightly notched structures.

The poorly exposed (only partly visible) first auxiliary lobe occurs in the middle of the outer half of the umbilical wall. So far as it is possible to see, this auxiliary (which is not shown in Neumayr and Uhlig's, 1881, Pl. XXVIII, fig. 1b, drawing) is only about one-third as long and considerably more narrow than the second lateral lobe. This adapically tapering lobe also is considerably less deeply denticulated than the second lateral lobe. Its tip is somewhat asymmetrically trifid. The fourth lateral saddle occurring in the middle of the umbilical wall is only slightly wider than the first auxiliary lobe and subdivided in two by a tiny, slightly notched lobule. The second, and the last, auxiliary lobe is situated within the inner half of the umbilical wall. This lobe, which is just as imperfectly exposed as the first auxiliary, appears to be a slender (about three times as long as wide), subparallel-flanked, only shallowly denticulated and apparently apically trifid structure. The length of this lobe appears to be about three-quarters that of the first auxiliary.

The second auxiliary lobe appears to be separated from the umbilical seam by only one tack-like shaped, slightly notched lobule, which is also only incompletely and poorly exposed.

The whole of this suture line, including its auxiliary part, is subradially oriented.

The external suture line of the holotype is closely matched by the much better exposed suture of an adult representative of *E. latissimus* from Sachsenhagen reproduced in Figure 14a. The lateral part of the latter suture only differs in a relatively widened, distinctly adapically tapering shape and proportions of both lateral lobes and in their markedly asymmetrically trifid terminations. This suture line confirms fully the exceptional width of the third lateral saddle and the shape and positions of the two auxiliary lobes. However, it differs in the presence of one extra, tack-like shaped lobule between the normally developed second auxiliary lobe and the considerably larger adumbilicalmost element. The latter may be accordingly interpreted as the underdeveloped third auxiliary lobe (Figure 14a). Furthermore, this suture line is subradially oriented throughout its extent.

The above described external suture lines of *E. latissimus* represent one morphological extreme. The other morphological extreme is exemplified by the suture of BGR, kv 370 (Figure 14b) that is characterized by very short and wide, much less deeply and elaborately denticulated lateral and auxiliary lobes. Its first and second lateral saddles are relatively much more narrow (i.e. only slightly wider than the preceding lobes) than those of the other morphological extreme (compare Figure 14a) but the remaining saddles are similarly wide. This external suture approaches the more sturdy and less elaborately denticulated sutures of *E. diplotomus* (e.g. Figure 16b) and the suture of *E.* aff. *laevis* (e.g. Figure 16c). It is, furthermore, morphologically transitional to the extremely sturdy and short lobed external sutures of *E. traillensis* and *E. laevis*. However, it differs from them in the parallel-sided character of all its lobes.

These two morphological extremes are connected by transitions (e.g. BGR, kv 369; Figure 14c). Therefore, they appear to reflect the infraspecific variability of the adult external suture line of *E. latissimus*.

Affinities and differences. *E. latissimus* has evolved from *E. diplotomus* and is the terminal representative of the *Euryptychites* lineage. It differs from *E. diplotomus* in the eucadicone shape and proportions of its shell and the absence of bidichotomous rib bundles. Its misidentification with younger polyptychitinid homoeomorphs, which are described elsewhere in this paper as representatives of *Hollwediceras* n. gen., is only possible when the two are compared superficially. Their differences are described below in the discussion of that genus. The *Euryptychites* species described from Greenland (Donovan, 1953) are characterized by different sculptural styles and a different external suture.

"Polyptychites" gravesiformis Pavlow 1892 from the D beds of the Speeton Clay is here placed in *Euryptychites latissimus* because of the close similarity of their sculpture and shell proportions and the character of the external suture line. Only the lateral lobes were figured by Pavlow (in Pavlow and Lamplugh, 1892, Pl. XIII, fig. 7c and Text-fig. on p. 493). However, his drawing shows the umbilical shoulder as cutting the middle lobule of the third lateral saddle. This suggests strongly that the auxiliary part of this suture line has only two lobes and that the umbilical seam cuts through the saddle that separates the second and the third auxiliary lobes. This interpretation is confirmed by Pavlow's (l. cit., p. 493) statement that following the second lateral saddle: "on remarque encore deux petites selles dans l'ombilic". The ventral and lateral lobes are about as wide as the adjacent saddles and sparsely and shallowly indented. The first lateral lobe distinctly tapers apicalward.

Euryptychites diplotomus (Koenen 1902)

Pl. 3, fig. 3; Pl. 19, fig. 3, Figures 15, 16a, 16b

*1902 *Polyptychites diplotomus* Koenen, p. 124-126, Pl. 54, fig. 3a, b; 4a, b.

1909 *Polyptychites gravidus* Koenen, p. 14-16, Pl. 1, Pl. 2.

1964 *Polyptychites (Propolyptychites) quadrifidus* Kemper, p. 23-24 (pars), Pl. 2, figs. 2, 3, Text-fig. 4.

1968 *Polyptychites quadrifidus* Kemper, p. 31, Pl. 12, fig. 3a, b (non fig. 7).

1976 *Polyptychites (Euryptychites) diplotomus* Kemper, p. 34, Pl. 8, fig. 1a, b.

1976 *Polyptychites quadrifidus* Kemper, p. 34, Pl. 12, fig . 3a, b (non Pl. 12, fig. 7).

Holotype. The original of Koenen (1902, Pl. 54, fig. 3a, b) in GIG collections.

Locus typicus. Muesingen near Bueckeburg.

Stratum typicum. *Platylenticeras*-Beds, lower lower Valanginian.

Material. 23 specimens in the collections of BGR, Hannover.

Diagnosis. *Euryptychites* species with an extremely variably shaped shell, which fluctuates from a moderately large and thick to a large and almost globular shape. The whorls remain high and are narrow rather than broadly arched in some representatives in comparison with characteristic examples of the genus. The ribbing is relatively fine. The coarsely ribbed variants exhibit a bidichotomous mode of rib splitting. The finely ribbed variants form quasifasciculate bundles that mostly consist of two secondary ribs. Each of these secondaries splits up with a considerable regularity into two tertiary ribs (so called diplotome bundling of Koenen, 1902).[1] The adult external suture line markedly ascendant throughout its extent.

Measurements (in mm).

Specimen	Whorl diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
Slender variant, BGR, kv 73	119	36(30)	37(31)	42(35)	67	83
Median variant BGR, kv 74	114	29(26)	38(32)	47(40)	67	50
Thick variant, BGR, kv 254	82	25(30)	27(35)	30(37)	52	69

Description. *E. diplotomus* represents a morphological and phylogenetical connecting link between *Propolyptychites* and the progressive *Euryptychites* species. In spite of this transitional character and a very great infraspecific variability, it is a good, well defined species which is restricted to the lower lower Valanginian. This species may even serve as an example of the variability of root-forms in their centers of evolutionary development.

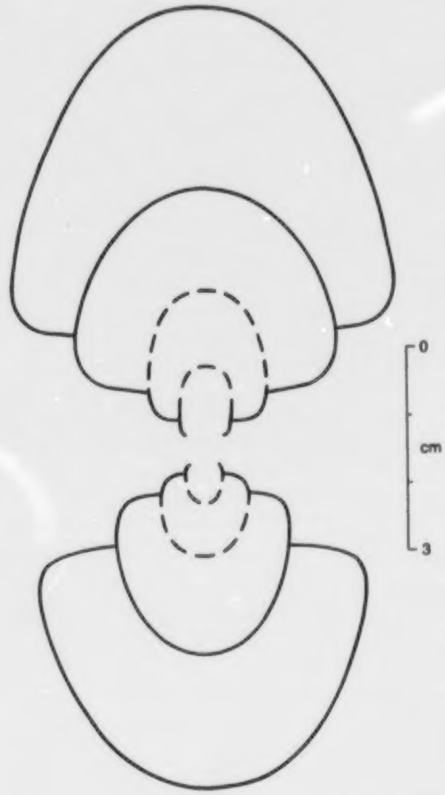

Figure 15. *Euryptychites diplotomus* (Koenen, 1902). Cross-section of an unnumbered specimen from Deilmann collection (private). Locality Suddendorf, Northwest Germany. Early early Valanginian. Note the linear scale.

All morphological features are variable and none of the 23 specimens agrees completely with any other. The species varies from an intermediate to a large size, though the largest whorl diameters do not appear to exceed 200 mm diameter. Because of scarcity of space only two relatively small, presumably incompletely grown specimens are figured here. They represent two sculptural extremes. Koenen's (1902, Pl. 54, figs. 3a, b; 4a, b) excellent figures are of larger specimens.

The whorl section varies from almost *Polyptychites*-like proportions to a cadicone morphology with low, arched whorls of considerable width. It was not possible to observe the ontogeny of the whorl cross-section on well preserved material. However, it is possible to assume with some probability that the cadicone proportions appear relatively late in the ontogeny (Figure 15). In the studied adult to almost adult shells the width of the whorl is always considerably greater than its height.

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[1] This "diplotome" bundling habit does not differ materially from the so called bidichotomous ribbing habit of *Dichotomites*. Therefore, this term won't be used further in this report.

The umbilical shoulder is broadly rounded in early and intermediate whorls. However, it is gradually transformed into a more or less sharpened rim in advanced growth stages as the shells become more and more cadicone. The umbilical wall gradually becomes higher and steeper at the same time. The umbilicus is step-like rather than funnel-like.

The external suture line of *Euryptychites diplotomus* conforms to that of other *Euryptychites* species in its most important features, such as the number of auxiliary lobes, but is rather variable in some details.

One morphological extreme, which is exemplified by specimen BGR, kv 332 (Figure 16a), features a suture line which conforms to that of the Sachsenhagen representative of *E. latissimus* (Figure 14a), except in its distinctly ascendant orientation throughout and a relatively greater development of its adumbilicalmost part. The second auxiliary lobe is almost as long as the first auxiliary lobe and is separated from the umbilical rim by an appreciably wider, more complexly denticulated fifth lateral saddle. However, the similarity of these two sutures includes the presence of an additional adumbilicalmost element that may be interpreted tentatively as an underdeveloped third auxiliary lobe (compare Figures 14a and 16a).

The other morphological extreme is exemplified by specimens BGR kv 333 and B 6-708 (Figure 16b) where all lateral saddles, including the third lateral saddle, become relatively narrowed, and ornamented with a lesser number of lobules while the lobes are relatively widened, shortened and less denticulated. Furthermore, the first auxiliary lobe of this suture is situated on the flank side of the shoulder. Finally, it includes only two auxiliary lobes that are distinctly constricted at the top, distinctly widened adapically and irregularly trifid.

The umbilical part of this suture line only differs from that of the other morphological extreme in a considerable widening of the fourth lateral saddle (correlative with the adventral displacement of the first auxiliary lobe) and a relative widening of the second auxiliary lobe. This variant of the suture line is just as markedly ascendant (15 to 20 degrees) throughout as is the other. This ascendant orientation of the external suture was observed in all three representatives of the species where the suture was studied. It appears to be a unique phenomenon in *Euryptychites*, diagnostic of *E. diplotomus* and at the same time reminescent of *Neocraspedites* s. str. This agrees with other evidence (see p. 42) which suggests that these two genera may have been derived from a common ancestor closely related to *E. diplotomus*.

Typical specimens are quite finely ribbed and have about 24-29 bullae per whorl. The bullae extend across the umbilical wall. In the early growth stages they extend radially to the umbilical seam, but on the following whorls they become increasingly obliquely inclined adorally. In the adult growth stage their morphology is variable. In most shells the bullae disappear rapidly on the outer third of the umbilical wall while in others they form pronounced, obliquely oriented swellings of the same width as the bullae proper.

Two specimens (BGR, kv 93 and BGR, kv 101) are more coarsely ribbed, with only about 17 bullae per whorl. They may represent a different species but material is too scarce for a definite conclusion.

The great majority of the specimens exhibit the name-giving "diplotomous" (i.e. bidichotomous) ribbing habit at least in the intermediate growth stages. Irregularities, such as the appearance of intercalated secondaries, do occur, particularly in the adult growth stage. Furthermore, the sculpture may become weakened on the flanks of some rare adult shells. In the intermediate growth stages bundles consisting of five secondaries may arise because of intercalation of a solitary rib between the two pairs of bifurcating secondaries. However, in these growth stages there also occur bundles consisting of an adapically situated dichotomous element and an adorally situated single secondary. The specimens exhibiting such bundles connect *E. diplotomus* with *E. traillensis* Donovan from Greenland. Finally, some finely ribbed specimens do not exhibit any well developed bidichotomous bifurcation of secondaries (BGR, kv 253). The rib bundles of such forms tend to have an almost fasciculate appearance with 4-5 secondaries (Pl. 19, fig. 3).[1]

Affinities and differences. *E. diplotomus* arose from *Propolyptychites quadrifidus* via palingenetic increase of the whorl width. The specimen figured by Kemper (1964, Pl. 2, fig. 3; Text-fig. 4) is a good example of such a transitional form connecting the genera *Propolyptychites* and *Euryptychites*. Because of its intermediate position, *E. diplotomus* does not exhibit the extreme development of diagnostic characters of *Euryptychites*, such as the very low and broadly arched whorls. Another diagnostic feature is the relatively refined and invariably bidichotomous sculpture on intermediate growth stages. This uniquely persistent bidichotomous sculpture represents an important distinction from *E. latissimus* and the younger homeomorphs of *Euryptychites*.

Euryptychites aff. *laevis* Donovan 1953

Pl. 26, fig. 6; Pl. 27, fig. 6; Pl. 28, fig. 1, Figure 16c.

Discussion. One representative of Northwest German *Euryptychites* (BGR, kv 363) studied by the writers differs substantially from the rest. It is best comparable with *E. laevis* Donovan (1953, p. 109, 110; Pl. 22, figs. 1a-1f) from East Greenland.

The shell is relatively narrow at first. However, it becomes strongly widened on the last preserved whorl. This whorl is septate to the end, so that the size of the adult shell is not known. The cross-section of the shell is *Euryptychites*-like. The umbilical shoulder is broadly rounded. The umbilical wall is high and is oriented almost perpendicular to the plane of symmetry in the proximity of the umbilical seam.

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[1] In the chapter dealing with the Northwest German taxa the term "secondaries" (or secondary ribs) is used commonly instead of that of "supplementary ribs" (compare p.13). Please keep this inconsistency in mind.

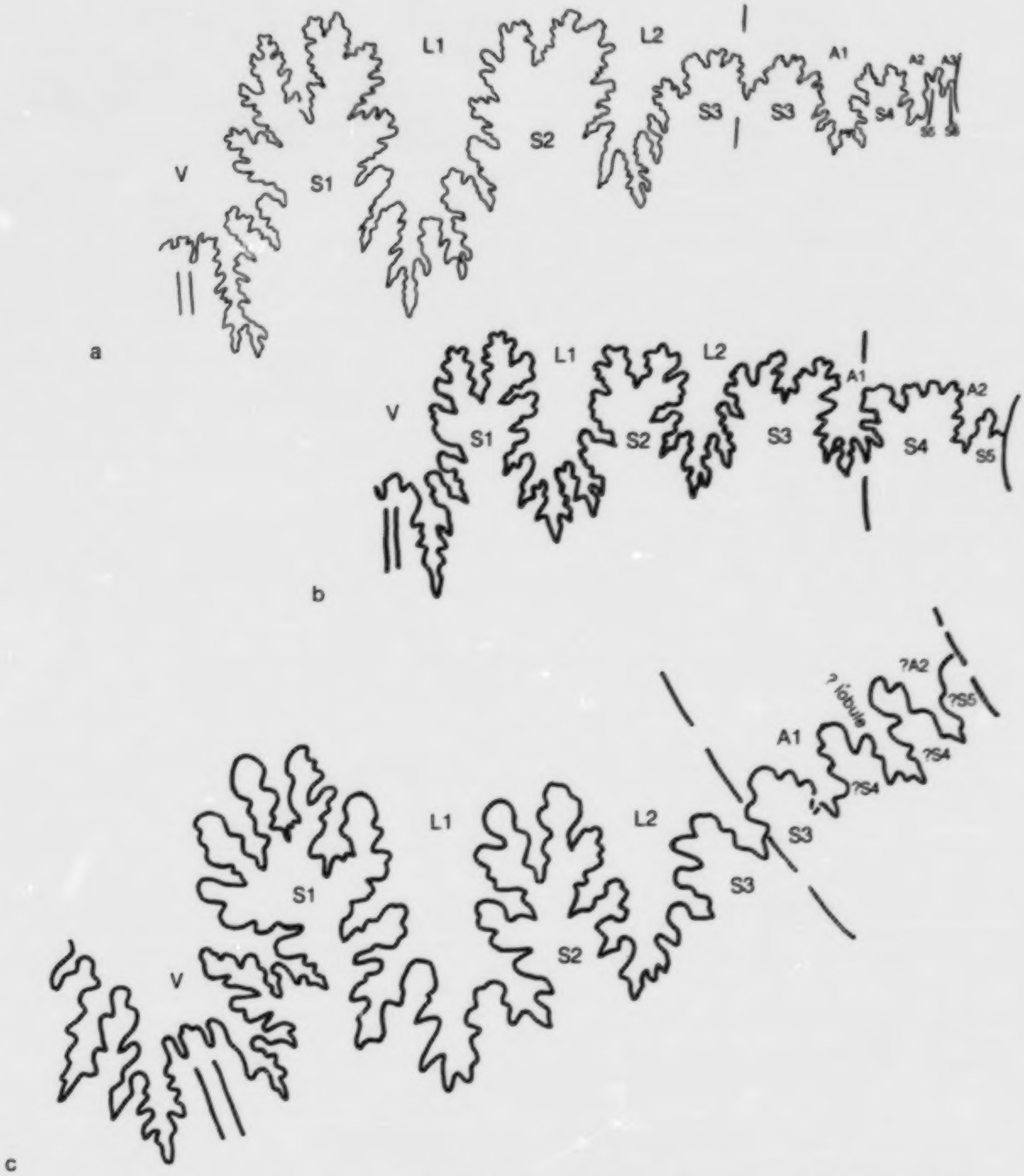
a
V
S1
L1
S2
L2
S3
S3
A1
S4
A2
A3
S5
S6
b
V
S1
L1
S2
L2
S3
A1
S4
A2
S5
c
V
S1
L1
S2
L2
S3
S3
A1
? lobule
?S4
?S4
?A2
?S5

Figure 16. Adult external suture lines of *Euryptychites diplotomus* (Koenen, 1902) and *E.* aff. *laevis* Donovan, 1953. **a.** *E. diplotomus*. Specimen BGR kv 332 from Sachsenhagen *Polyptychites* beds, ?Early Valanginian. Early adult suture observed at the whorl height (wh) of about 26 mm, x 2.5 (approx.). **b.** *E. diplotomus*. Specimen B6/708, Geol. Inst. Muenster, from Sachsenhagen, Northwest Germany. *Platylenticeras*-beds, early Valanginian. Early adult suture observed at the whorl height (wh) of 28 mm, x 2 (approx.). **c.** E. aff. *laevis*. Specimen BGR, kv 363 reproduced in Pl. 26, fig. 6; Pl. 28, fig. 1 (see their explanations for further details). Early adult suture observed at the whorl's height (wh) of about 37 mm, x 2 (approx.).

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
BGR, kv 363	84	23(27)	25(30)	37(44)	43	60

The external suture line is characterized by long and strongly denticulated elements (Figure 16c). Only two lobes — the first and the second laterals — are situated adventrally of the umbilical shoulder. The saddles which separate these lobes are relatively narrow and subdivided by pronounced and long lobules. The imaginary line connecting the tops of the saddles on the venter and its extension to the umbilical shoulder is ascendant and forms an angle of 20° with the corresponding shell radius. The third lateral saddle situated on the broadly rounded umbilical shoulder is subdivided by a pronounced median lobule into two approximately equal, narrow parts.

The elevated umbilical wall is occupied by three approximately equally-sized lobes which are separated by long and narrow saddles (Figure 16c). It is impossible to decide whether one of these lobes represents an intervening lobule, so it is uncertain whether there are two or three auxiliary lobes on the umbilical wall. However, a comparison with the corresponding parts of external suture lines of other *Euryptychites* species, including *E. laevis* (see Donovan, 1953, Pl. 22, fig. 1e; Text-figure 9), which consistently exhibit only two auxiliary lobes, suggests the presence of only two auxiliaries separated by an abnormally (perhaps pathologically?) enlarged lobule.

The imaginary line connecting the tops of the saddles exposed on the umbilical wall is oriented radially. Therefore, it meets at an obtuse angle the imaginary line connecting the tops of the saddles on the ventral side and the flank of our specimen. The resulting abrupt knick of the lines is situated exactly on the umbilical shoulder.

The sculpture is coarse. The contrast between the feebly developed bullae and coarse ribs is especially prominent. The adapical half of the last preserved whorl has 8 to 9 primary elements, which can hardly be named bullae. These elements are slightly inclined backwards. They give rise to 2 to 3 coarse supplementary ribs. Solitary, intercalated secondaries, which extend addorsally without any subdivision, occur between these simple bundles. The supplementary ribs are also bent backwards on the flank but acquire short forward bends on the venter. The bullae disappear on the oral half of the last preserved whorl. Those parts of supplementary ribs situated nearest to the umbilicus also disappear there so that the adumbilical parts of the flanks become smooth. Similar sculptural changes occur also in the *E. laevis* from East Greenland. The decline of sculpture begins on ontogenetically still earlier growth stages in this species. However, its bullae exhibit pronounced forward bends instead of backward bends characteristic of the German specimen. The latter exhibits so many morphological peculiarities (compare also the suture line) in comparison to other German representatives of *Euryptychites* that one must consider the possibility of its being a pathological specimen.

Genus *Neocraspedites* Spath 1924

Type species. *Neocraspedites semilaevis* (Koenen 1902) by original designation (Spath, 1924, p. 74).

Diagnosis. Slender Polyptychitinae in which the cross-section has subparallel to strongly convergent flanks in combination with a narrowly arched venter. The flanks are feebly to moderately convex. The ribbing is fine and has a pronounced tendency to disappear in the flank's middle on intermediate and advanced whorls where the sculpture consists of a "crown" of low and refined bullae on the umbilical shoulder and a "crown" of supplementary ribs on the ventral shoulders and venter. Contrary to other genera of the *Propolyptychites*-phase, the density and number of ribs either does not decrease or decrease only insignificantly in the adult growth stage. The adult external suture line is markedly ascendant throughout and has three auxiliary lobes.

Discussion. Spath (1924, p. 75, footnote 5) erected the generic name *Neocraspedites* for slender "*Craspedites*-like developments of *Dichotomites*" which lose the sculpture on the flanks. It was necessary to differentiate nomenclatorially the younger *Craspedites*-like ammonites from the older true *Craspedites* as it was customary (especially in Koenen, 1902) to apply the latter name to Valanginian and Hauterivian ammonites which only mimic *Craspedites*.

The Olcostephanidae have thrown off several *Neocraspedites*-like offshoots in the course of their evolution. However, Spath (1924) knew only those lineages which were derived from *Dichotomites* s. lato and *Simbirskites* s. lato. He introduced the name *Craspedodiscus* for the last lineage. It was not known at the time that there are also *Craspedites*-like polyptychitinids of an early early Valanginian age. The existence of this offshoot was pointed out by Kemper in 1973. There is no doubt at all that the *Craspedites*-like olcostephanids of the Valanginian and Hauterivian belong to three independent lineages, which are not directly connected genetically. Their similarity is caused entirely by a convergent evolution.

The situation is complicated by the circumstance that Spath (1924) selected the species "*Craspedites*" *semilaevis* Koenen as the type of *Neocraspedites*. This species is most likely derived from the *Platylenticeras*-Beds and is thus an early early Valanginian form. Therefore, the type species represents a *Craspedites*-like development not of *Dichotomites* (Spath, loc. cit.) but of *Propolyptychites* Kemper. All other "*Craspedites*" species described by Koenen (1902) and placed in *Neocraspedites* by Spath are, in contrast, latest early and late Valanginian allies of *Dichotomites* s. lato; they are: "*C.*" *fissuratus*, "*C.*" *undulatus*, "*C.*" *complanatus* and "*C.*" *flexicosta*. The same is true also of "*Neocraspedites*" *speetonensis* Spath and the "*Neocraspedites*" species cited in the Russian literature. All these species must be placed in *Prodichotomites* Kemper 1973 (see Kemper, 1973, 1975, 1976, 1977 for further details) and *Neocraspedites* should be used only for *Craspedites*-like ammonites from the lower lower Valanginian. This genus includes *N. semilaevis* (Koenen), *N. semisulcatus* (Koenen), *N. undulatocostatus* Donovan, *N. greenlandicus* Donovan and some species which are figured in this paper under open nomenclature.

Neocraspedites, in this sense, includes small to medium-sized ammonites with narrowly umbilicate and slender shells. Only in *N. undulatocostatus* are the whorls fairly thick.

Neocraspedites evolved from the same ancestors as the similarly fine ribbed *Paratollia* species — *P. tenuicostata* Kemper and *P. emslandensis* Kemper, which explains some of its similarities with these forms.

The convergent *Prodichotomites* species usually differ from the true *Neocraspedites* in being still more slender and more involute. Furthermore, they are, as a rule, even more finely ribbed. Their tertiary ribs split up closer to the venter whilst the secondary ribs commonly persist longer in the zone devoid of the sculpture than those of *Neocraspedites*.

Neocraspedites is recorded only from the Lower Saxony Basin and eastern Greenland. However, one has to postulate that it probably occurs also in the North Sea Basin. The previous quotations of craspeditid ammonites from the D4-unit of Speeton (Spath, 1924, p. 75: "*Craspedites fragilis*") refer to the genus *Bodylevskites* as interpreted here instead of *Neocraspedites*.

As with other early early Valanginian polyptychitinids of Northwest Europe, the external suture line of *Neocraspedites* is insufficiently understood. Of the Northwest German representatives of the genus only the suture line of its type species *N. semilaevis* (Koenen 1902) has been figured. The suture line of the East Greenland *N. greenlandicus* Donovan is the only other one known.

The authors were able to confirm the correctness of Koenen's (1902, Pl. V, figs. 9, 10) drawings of the external suture line of *N. semilaevis* on the original of the holotype and on that of another unnumbered example of the species from the Sachsenhagen clay pit. These two specimens are in GIG collections.

The external suture line of *N. semilaevis* is morphologically much more advanced than the sutures of any other early early Valanginian polyptychitinid taxon known. First of all, the imaginary line connecting the tops of its elements is strongly and almost evenly (slightly less so within the umbilicus) ascendant throughout. It forms a 25 to 30° angle with the corresponding shell radius (Koenen, 1902, Pl. V, fig. 9). Furthermore, not only the first and second lateral lobes but also the first auxiliary are situated on the whorl flank. The first auxiliary is situated at about the top of the umbilical bulla. The length of the bulla and the whole span of the umbilical shoulder are occupied by a markedly widened 4th lateral saddle (about four times wider than the preceding first auxiliary lobe; Koenen, 1902, Pl. V, fig. 10). Yet another distinction consists in the presence of two more auxiliary lobes (second and third) on the umbilical wall. The first is situated in the middle while the second is barely exposed at the umbilical seam. Finally, the termination of the first lateral lobe is almost exactly bifid, in contrast to the symmetrically to asymmetrically trifid termination of this lobe in other early early Valanginian polyptychitinids. However, there are exceptions to this rule, as indicated by the adult external suture shown in Figure 13b. This suture shows only two auxiliary lobes.

The external suture line of *Neocraspedites greenlandicus*, which was figured in part by Donovan (1953, Pl. 23, fig. 4a) and also studied by the writers in its plastotype, does not differ materially from that of *N. semilaevis* in any of the diagnostic features. Its markedly and approximately steadily ascendant orientation (about 30° in relation to the corresponding shell radius), the presence of three lobes on the whorl flank and the almost exactly bifid termination of the first lateral lobe are exactly reproduced in Donovan's (1953) photograph. The unfigured umbilical part of the suture line is also markedly ascendant and consists of the second and third auxiliary lobes, the first of which is situated close to the umbilical shoulder while the last is situated near the middle of the wall.

As the two suture lines are so similar, they are interpreted tentatively as being diagnostic of the genus as a whole. On this basis *Neocraspedites* differs sharply from the true *Euryptychites*, *Propolyptychites* and all of the early, more primitive representatives of *Polyptychites*. All of these are characterized by a subradial to only feebly (and at that impersistently) ascendant orientation of the external suture line, presence of only two lobes (i.e. first and second laterals) on the shell's flank and the presence of only two auxiliary lobes, which are both situated on the umbilical wall. It is these distinctions of the suture line that are critical for the substantiation of a full generic separation of *Neocraspedites* from the otherwise very closely similar *Propolyptychites*.

The suture line of *Neocraspedites* is much more similar to the suture lines of the late, morphologically advanced representatives of *Polyptychites* (i.e. its *P. orbitatus-tethyale* species group) and the genera *Dichotomites* and *Prodichotomites* Kemper 1971 as most of these taxa possess at least three auxiliary lobes, of which the first is situated on the whorl flank. However, none of them are known to possess sutures that are markedly ascendant throughout their length or have bifid first lateral lobes. In combination with a considerable time gap separating *Neocraspedites* from late, morphologically advanced *Polyptychites*, *Dichotomites* and *Prodichotomites*, and the well established derivation of these taxa from other polyptychitinids, these distinctions reveal the entirely homoeomorphic character of their suture lines.

The considerably more advanced character of the external suture line of *Neocraspedites* in comparison with that of the Northwest European and North Siberian representatives of *Bodylevskites* Klimova 1978 does not permit derivation of this otherwise closely morphologically similar genus from *Neocraspedites*. This conclusion suggests, in turn, that such younger North Siberian polyptychitinid taxa as *Siberiptychites* and *Astieriptychites*, the external suture lines of which are similar to that of *Neocraspedites* s. str., are not directly related to this genus either.

Neocraspedites semilaevis (Koenen 1902)

Pl. 1, fig. 2; Pl. 2, fig. 3; Figure 13b.

*1902 *Craspedites semilaevis* Koenen, p. 80-82, Pl. 5, figs. 8-10.

1957 *Neocraspedites semilaevis* Wright in Arkell et al., p. L348-L349, Fig. 457-4a-4b.

1958 *Neocraspedites semilaevis* Luppov and Drustchits, (in Khimiashvili et al., 1958) p. 94, Pl. 42, figs. 5a, b.

1976 *Neocraspedites semilaevis* Kemper, p. 34, Pl. 23, fig. 11.

Holotype. The original of the specimen figured by Koenen (1902, Pl. 5, figs. 8-10), in GIG collections, Cat. no. 451-5.

Locus typicus. Osterwald ("Tiefbauschacht").

Stratum typicum. Is not absolutely certain. However, is most likely the *Platylenticeras*-Beds (lower lower Valanginian).

Material studied. 16 specimens from Osterwald, Sachsenhagen, Muesingen and Suddendorf.

Diagnosis. A typical species of *Neocraspedites* with a fine sculpture. The weakening of sculpture on the flanks may be differently expressed depending on the either more or less advanced morphology of individual specimens; it is, however, always clearly developed. The shape of the shell is variable and ranges from moderately thick whorls with distinctly convex flanks to very slender whorls with subparallel flanks.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
Holotype	64	10(16)	23(36)	32(50)	16	25
BGR, kv 255	93	19(20)	33(35)	44(47)	27	35
BGR, kv 256 (a thick variant)	78?	20(26)	28?(36)	33?(42)	32?	40

Description. As is apparent from the measurements, the shell shape is rather variable. The holotype (Koenen's (1902, pl. 5, figs. 8-10) drawing is an excellent likeness) is an advanced form with a slender shell, particularly narrow umbilicus and a strongly expressed weakening of the sculpture. It is chambered to the end, but the adult size of the species can be estimated from other material and ranges from 80 to 120 mm.

The other non-measurable features of the shell are also rather variable. The venter is narrowly rounded. The whorl cross-sections of the more conservative representatives of the species have adventrally convergent flanks. Their greatest width is situated at the level of the umbilical shoulder. The morphologically more progressive representatives have subparallel and only slightly convex flanks. The largest widths of the inner whorls of these forms, as for example of the holotype, may be situated considerably higher than the umbilical shoulder. This results in the whorl cross-section becoming high-oval rather than trapezoidal. The umbilical shoulder of the inner whorls is broadly rounded. It is, however, less rounded and forms a distinct rim in the intermediate and adult growth stages. The umbilical wall, which is strongly inclined (relative to the plane of symmetry) and low in the juvenile growth stage, becomes gradually higher and forms an ever greater angle with the plane of symmetry in the course of ontogeny. In the specimen reproduced in Pl. 2, fig. 3 this shoulder even becomes perpendicular to this plane in the adult state. In this specimen the last whorl covers about 72 per cent of the preceding whorl. This overlap (i.e. involution) increases to 85 per cent in the holotype. The always narrow umbilicus invariably remains step-like in spite of such a great overlap of the whorls.

For description of the suture line see the generic description.

As with the shape of the whorl, the sculpture shows strong variation. It is dense and consists accordingly of relatively fine elements. The bullae are always expressed as low protuberances on the umbilical shoulder. They are pronouncedly bent forward on the umbilical wall and have accordingly a comma-like appearance. This bend disappears before the middle of the umbilical wall. The number of the bullae varies from 14 in the holotype to 22 in the specimen reproduced in Pl. 2, fig. 3. As a rule, it amounts to 18.

The *Craspedites*-like weakening of the sculpture on the flanks begins early in ontogeny. It results in an opposition of a "crown" of bullae to that of more refined ribs covering the upper flanks and the venter on either side of a smooth zone in midflank. This results in an indistinct development of the bundling ribs. This bundling style appears to range from bidichotomous bundles to those with several additional intercalated secondary ribs, which are characteristic of the morphologically progressive specimens. The adventral ribs of the holotype are the coarsest known. They are also more strongly bent forward on the ventral shoulder and venter than those of any other shell studied. The holotype belongs, therefore, to the most progressive variant of the species in this respect also. In other specimens studied the forward bend of supplementary ribs on the venter is either only moderately developed or absent.

The figured material of *N. semilaevis*, other than the holotype, is preserved in the BGR collections, Cat. nos. kv 257-259.

Affinities and differences. The species exhibits some morphological similarities with some early Polyptychitinae, such as *Paratollia emslandensis* Kemper and *Paratollia tenuicostata* Kemper. Its derivation from this species group is inferred accordingly. However, both of these *Paratollia* species retain strong ribbing throughout their ontogeny. The differences from *N. semisulcatus* (Koenen) consist, in particular, in a smaller size, more slender shell proportions, a finer ribbing, and an earlier appearance of the weakening of sculpture on the flanks. *N. undula-*

tocostatus (Donovan) resembles *N. semilaevis*, except for being considerably thicker.

Neocraspedites n. sp. aff. *semilaevis* (Koenen)

Pl. 1, fig. 1; Pl. 2, fig. 4

Discussion. It is questionable whether or not the two *Neocraspedites* specimens assigned to *N.* n. sp. aff. *semilaevis* (Koenen) fall into the range of morphological variation of that species. One of them — a juvenile shell (Pl. 2, fig. 4A, B) — is relatively thick and differs in its particularly fine ribbing habit. The other specimen (Pl. 1, fig. 1) has a relatively coarse adventral sculpture and its umbilical shoulder is sculptureless and broadly rounded in the adult growth stage.

Neocraspedites greenlandicus Donovan 1953

1953 *Neocraspedites greenlandicus* Donovan, p. 113, Pl. 23, fig. 4.

Discussion. As already mentioned in the generic description, *Neocraspedites greenlandicus* is interpreted herein as a thick development of *Neocraspedites* s. str. It is believed to occur in the local equivalents of the upper *Platylenticeras*-Beds of the Lower Saxony Basin.

Neocraspedites semisulcatus (Koenen 1902)

Pl. 3, fig. 1

•1902 *Polyptychites semisulcatus* Koenen, p. 92, 93, Pl. 2, fig. 1.
?1902 *Polyptychites keyserlingi* Koenen, p. 131, Pl. 2, fig. 2, 3.

Holotype. The original of specimen figured by Koenen (1902, Pl. 2, fig. 1), GIG collections.

Locus typicus. Osterwald.

Stratum typicum. Not known definitively but most likely *Platylenticeras*-Beds (lower lower Valanginian).

Material. In addition to the holotype, two specimens from Sachsenhagen.

Diagnosis. Medium-sized to large species of *Neocraspedites* with ribs that are coarse rather than fine. The weakening of the sculpture begins only relatively late in the ontogeny. The flanks are feebly convex but convergent adventrally.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
BGR, kv 260	135	27(20)	47(35)	61(45)	45	57

Description. The holotype is a very large ammonite with a shell diameter of about 300 mm; Koenen's figure (1902, Pl. 2, fig. 1) is strongly reduced. The character of intermediate and early growth stages cannot be studied in the holotype. The figured lateral part of its suture line (Koenen, 1902, Pl. 2, fig. 1) appears to agree with that of *N. semilaevis*, except that the second lateral lobe is situated on the lowermost part of the flank. The structure of the auxiliary part of the suture line remains unknown.

The specimen figured in this paper (BGR, kv 260; Pl. 3, fig. 1) apparently represents the morphology of intermediate growth stages. The flanks of the last preserved whorl are only slightly convex and merge into a narrow but obtusely rounded venter. The greatest width of the cross-section is situated in the proximity of the rounded umbilical shoulder. The umbilical wall is strongly convex on the early whorls and the penultimate whorl. However, it is only slightly convex on the ultimate preserved whorl. In spite of the rounded umbilical shoulder and the convex umbilical wall, the narrow umbilicus (about 20 per cent) appears to be step-like rather than funnel-like.

The moderately strong ribs are still connected with the bullae at the beginning of the last preserved whorl. So far as one can see, two to three secondary ribs branch off one bulla. These secondaries then split into two tertiaries considerably closer to the ventral shoulder. The typical *Neocraspedites*-like reduction of the sculpture on the flanks begins within the first quarter of the last whorl. From there on the sculpture consists only of the bullae and a "crown" of secondary ribs on the ventral shoulders and the venter. The secondary ribs bend forward on the flank but then cross the ventral shoulder and venter radially. The penultimate whorl is ornamented by 19 bullae while the ultimate has 17 bullae, which form pronouncedly comma-like bent protuberances. They are elevated in a typical bullate fashion on the penultimate whorl. However, on the ultimate whorl they become lower and therefore appear to be more like welts. The bullae extend onto the umbilical wall where they reach almost to the umbilical seam. These extensions are moderately bent forward in the intermediate growth stages. However, they become progressively more and more bent forward on the outer whorls.

Affinities and differences. The species is a descendant of *Propolyptychites quadrifidus* (Koenen) and the two are connected by transitional forms. This lineage parallels that leading to *N. semilaevis* (Koenen). The distinctions from *N. semilaevis* are discussed in its description.

Neocraspedites undulatocostatus (Donovan 1953)

1953 *Polyptychites undulatocostatus* Donovan, p. 104, Pl. 1, fig. 5.

Discussion. The general appearance of this East Greenland species, which was originally assigned to *Polyptychites* by Donovan (1953, p. 104), resembles greatly that of *Neocraspedites* species from the *Platylenticeras*-Beds of Northwest Germany. It differs from the latter in the considerable thickness of the whorls. However, some *Neocraspedites* specimens from Northwest Germany have even thicker whorls (e.g. the shell BGR, kv 256) and so deviate equally strongly from its typical representatives.

Therefore, and because of the character of its external suture line discussed in the description of the genus *Neocraspedites,* there is no doubt that *N. undulatocostatus* from East Greenland forms part of the species group of true *Neocraspedites* from the early early Valanginian.

Genus *Propolyptychites* Kemper 1964

Diagnosis. A morphologically variable group of narrowly umbilicated Polyptychitinae which posses "quadrifidous"[1] (=diplotomous = bidichotomous) rib bundles at least in the intermediate growth stages.

Type species. Polyptychites quadrifidus Koenen 1902.

Discussion. The genus includes early Polyptychitinae, so far only found in the Lower Saxony Basin and the North Sea region (Heligoland). Except for *E. diplotomus* Koenen and *P. quadrifidus* Koenen, these early Polyptychitinae of the *Platylenticeras*-Beds were unknown until a few years ago when they were described by Kemper (1964, 1968, 1973, 1976). The locality that yielded the fossil material critical for the understanding of *Propolyptychites* is Suddendorf near Bentheim in the German-Dutch boundary zone. These oldest known Polyptychitinae and their closely related contemporary allies are particularly remarkable because of the prevalence of already strongly specialized, adaptive forms with narrow umbilici, as for example in *Neocraspedites*, *Euryptychites*, and representatives of the species group of *Propolyptychites bentheimensis*. All their species exhibit a great variability characteristic of a rapidly evolving stock in its typogenic phase (Schindewolf, 1947, p. 15, 16).

The genus embraces the following lineages:

(1) The most likely polyptychitinid ancestral forms around *Propolyptychites quadrifidus* (Koenen), from which may be derived the true *Polyptychites* species of the "*Polyptychites*-Beds"; and
(2) *Propolyptychites bentheimensis* Kemper.

Considering the great variability of the morphological features of *Propolyptychites*, it is remarkable that all its species exhibit — in at least one of their growth stages — a bidichotomous mode of bundling. The strength of ribbing varies from moderately strong to fine and the bullae are slight rather than prominent in all species.

The presence of a bidichotomous mode of bundling and the weak development of bullae in combination with a narrow umbilicus permits a differentiation of *Propolyptychites*, including its coarsely ribbed representatives, from the younger *Polyptychites* Pavlow. The superficially similar *Subpolyptychites* Sazonova and *Chandomirovia* Sazonov belong to the Craspeditidae. They differ first of all in their diagnostic craspeditid suture line. However, they can be distinguished also in the absence of a suture line. Though these two genera, as well as *Surites*, do exhibit a bidichotomous mode of bundling, the subdivision of their primaries occurs very regularly and rather high on the flank. Furthermore, these craspeditid genera differ in a marked forward swing of the secondaries on ventral shoulders and venter, which is absent in the *Propolyptychites* species.

The external suture line of *Propolyptychites* is insufficiently understood. The suture of the holotype of *P. quadrifidus* (Koenen) (1902, Pl. III, fig. 1D), which is the only one figured previously to the best of the writers' knowledge, is among the most primitive (and at the same time the most olcostephaninid-like) in the subfamily Polyptychitinae. All of its lobes are relatively shorter and wider in comparison with those of all other polyptychitinids, except for those of *Euryptychites traillensis* and *E. laevis*. Furthermore, these lobes are only sparsely and shallowly denticulated and taper markedly adapically. The saddles are always considerably to much wider than the preceding lobes. Only first and second lateral lobes are situated on the whorl flank. The markedly adventrally inclined first auxiliary lobe (Koenen, 1902, Pl. III, figs. 6, 10), which is separated from the second lateral lobe by an unusually wide second lateral saddle (it is at least three times wider than the second lateral lobe), is situated already on the outermost part of the umbilical wall, next to the rounded umbilical shoulder. It is followed by only one small, slightly notched auxiliary lobe which is situated hard at the umbilical seam. As already mentioned in the description of *Euryptychites*, the overall morphology of this primitive suture line of *Propolyptychites quadrifidus* indicates its being an ancestor of that genus. This morphology is equally compatible with the direct derivation from *Propolyptychites* of the oldest and most primitive representatives of *Polyptychites*, which also exhibit widely lobed, shallowly denticulated suture lines with only two auxiliary lobes (e.g. *P. brancoi*, older forms of *P. keyserlingi*, etc.). As pointed out in the description of the genus *Polyptychites*, this evolutionarily primitive external suture line in its early representatives gradually changes into a more advanced suture line in its younger species (e.g. the so called *Polyptychites* ex gr. *orbitatus-hapkei* of latest early and earliest late Valanginian).

The external suture line of the holotype of *Propolyptychites bentheimensis*, figured here for the first time (Figures 17a, 17b) is of the same primitive type as that of *P. quadrifidus*. Its second auxiliary lobe is not exposed and is assumed to be situated at the umbilical seam. The presumably adult suture reproduced in Text-figure 17b is considered to be typical of the genus. However, the sutures of *P. bentheimensis* are variable and include more advanced, essentially *Polyptychites*-like examples (Figure 17a) with relatively much more long and slender, subparallel-flanked lobes.

The ancestors of *Propolyptychites* should be sought presumably among the Spiticeratinae of the Tethyan Realm, which penetrated into the present North Sea region via Poland. *Peregrinoceras* sensu Casey 1973 and

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[1] This "quadrifidous" bundling habit does not differ materially from the so called bidichotomous ribbing habit of *Dichotomites*. Therefore, the former term won't be used in this paper.

Bodylevskites ex gr. *pumilio* (Vogel 1959) could be connecting links between the two taxa.

Propolyptychites quadrifidus (Koenen 1902)

Pl. 4, fig. 1; Pl. 4, fig. 7

*1902 *Polyptychites quadrifidus* Koenen, p. 109-110, Pl. 3, figs. 6, 7, 10.

1964 *Polyptychites (Propolyptychites) quadrifidus* Kemper, p. 23-24 (pars), Pl. 1, fig. 4 *(non* Pl. 2, figs. 2, 3).

1968 *Polyptychites* ("*Propolyptychites*") *quadrifidus* Kemper, p. 31, Pl. 12, fig. 7 (*non* fig. 3a, b).

1976 *Polyptychites quadrifidus* Kemper, p. 34, Pl. 12, fig. 7 *(non* Pl. 12, fig. 3a, b).

Holotype. The specimen reproduced by Koenen (1902, Pl. 3, fig. 6, 7, 10) through monotypy; it is in GIG collections.

Locus typicus. Osterwald.

Stratum typicum. Not established with an absolute certainty but is most likely the *Platylenticeras*-Beds (lower lower Valanginian).

Material. 6 specimens from Osterwald, Suddendorf and Sachsenhagen.

Diagnosis. A medium-sized species with a variable morphological appearance. The whorls are slender to moderately thick and ornamented with bidichotomous rib bundles at least in the intermediate growth stages.

Discussion. The mode of preservation of the specimens available does not permit any measurements. The species is not described here as Koenen (1902) gave a detailed description of the holotype.

Propolyptychites quadrifidus is a variable species which is connected by transitional forms with other species of the *Platylenticeras*-Beds. Transitional forms to *Euryptychites diplotomus* (Koenen) were figured by Kemper (1964, Pl. 2, figs. 2, 3; 1976, Pl. 12, fig. 3a, b). Transitional forms to *Neocraspedites semisulcatus* (Koenen), *Pr. bentheimensis* Kemper and *Paratollia tenuicostata* were also observed. The species differs from the true *Polyptychites* species in the presence of bidichotomous rib bundles, at least in the intermediate growth stages.

The species is one of the few among the Polyptychitinae in which the ontogeny is known (Kemper, 1964, Pl. 1, fig. 4; 1976; Pl. 12, fig. 7 and this paper Pl. 4, fig. 7). The sculpture is feebly developed to a shell diameter of 12 mm, where the bullae make their first appearance. The ribbing habit is distinctly bidichotomous already at shell diameter of 20 mm.

The external suture line was already described in the discussion of the genus *Propolyptychites*.

Affinities and differences. The characteristic feature is the prevalence of a bidichotomous bundling habit in relatively small shells with low whorls. The transitional forms and genetic relationships have already been discussed.

Propolyptychites bentheimensis Kemper 1976

Pl. 2, fig. 1; Figures 17a, 17b

1963 *Polyptychites convolutus* Kemper, p. 478, Pl. 36, fig. 3.

1968 *Polyptychites ascendens* Kemper, p. 31, Pl. 1, fig. 5.

*1976 *Polyptychites bentheimensis* Kemper, p. 34, Pl. 1, fig. 5; Pl. 30, fig. 2.

Holotype. The specimen reproduced by Kemper (1976, Pl. 1, fig. 5) by original designation. It is in BGR collections, kv 57.

Locus typicus. Suddendorf near Bentheim.

Stratum typicum. Upper *Platylenticeras*-Beds, lower lower Valanginian.

Material. 11 poorly preserved specimens from the localities Suddendorf and Sachsenhagen.

Diagnosis. A variable *Propolyptychites* species with a relatively slender to, at the very most, moderately thick whorls and a moderately involute umbilicus. Adult sculpture exhibits characteristic forward bends of the ribs on the flanks. Umbilical wall is only moderately strongly inclined. The suture line is conservative polyptychitinid but has three lobes on the flank and is relatively ascendant.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
Holotype, BGR, kv 57	107	28(26)	36(32)	47(43)	50?	60
Specimen, BGR, kv 66	100	28(28)	34(34)	40(40)	—	—

Description. The holotype is a morphologically progressive variant. Therefore, it exhibits well the characteristic features of the species. Only the living chamber and the last suture line of the holotype are preserved. According to all indications, it represents the adult growth stage. The living chamber has a length of at least three-quarters of a whorl. The largest diameter is 110 mm and the species can accordingly be classified as being of a moderately large size. Other specimens show that the maximum shell diameter reaches about 150 mm.

The whorl is broadly rounded and the venter is shaped rather like a Roman arch at the beginning of the living chamber. The whorl width is considerably greater than the height: its greatest width is at the level of the umbilical shoulder. The height of the whorl increases somewhat on the last part of the living chamber. The umbilical shoulder is rounded. The umbilicus, which comprises 26 per cent of the shell diameter, is relatively narrow (moderately involute). The umbilical wall is low and only moderately steeply inclined.

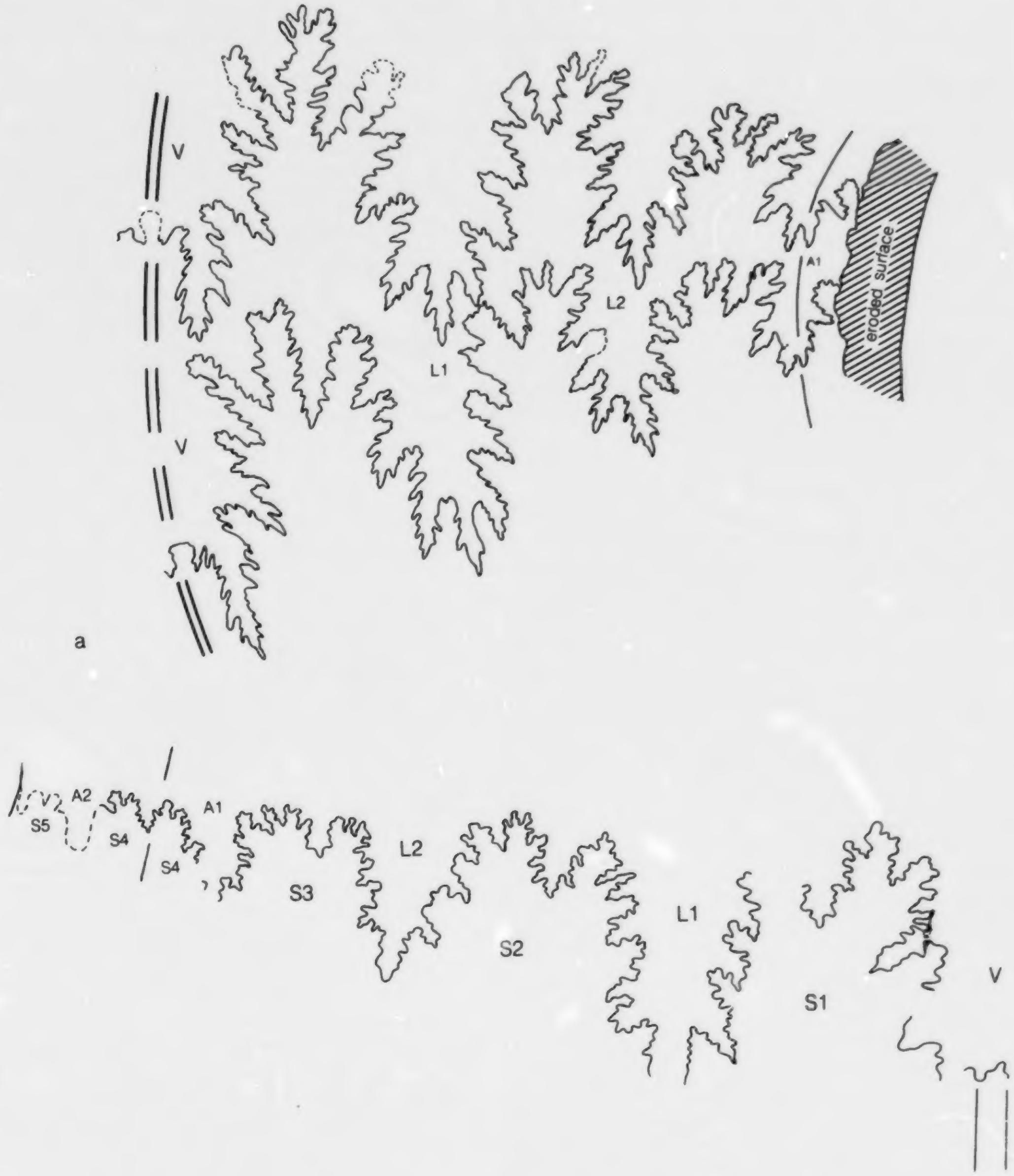

Figure 17. Adult external suture of *Propolyptychites bentheimensis* Kemper, 1976. **a**. Otherwise (i.e. in this paper) unfigured specimen BGR, kv 47 from Suddendorf, Northwest Germany. Two advanced adult sutures occurring 1/4 whorl before the beginning of the adult living chamber at the shell diameter of about 61 mm, x 3 (approx.). **b**. Otherwise unfigured holotype BGR, kv 57 from Suddendorf near Bentheim, Northwest Germany. upper *Platylenticeras*-Beds, early early Valanginian. The terminal adult suture just before the adult living chamber at the whorl height of about 35 mm, x 8, 5 (approx.).

The incompletely known adult external suture line (Figures 17a, 17b) is inferred to be typically polyptychitinid where the number of lobes is concerned. It has, as a rule, three lobes on the flank and is believed to have only one lobe (i.e. the second auxiliary; see Figure 17b) in the middle of the umbilical wall. However, this remains insufficiently documented as the umbilical parts of all suture lines studied are poorly preserved. The first auxiliary lobe may straddle the umbilical shoulder in some other specimens (e.g. Figure 17a). The shape of the lobes and the degree of their denticulation are variable. The holotype (Figure 17b) represents one extreme characterized by short and sturdy, partly tapering lobes, which are sparsely and shallowly denticulated. All lateral saddles are much wider than the preceding lobes. This conservative variant resembles the adult external suture line of *Paratollia* (Figure 13a). The other morphological extreme is characterized by considerably more slender and longer lobes, which are richly and deeply denticulated. All lateral saddles are much more narrow than those of the holotype; they are either about as wide as the preceding lobes or appreciably more narrow. This progressive variant is essentially *Polyptychites*-like.

On the living chamber the sculpture is developed in a fashion typical for the species, the ribs being strongly forwardly arched (forwardly convex) on the flanks. The low bullae are strongly inclined forward and forwardly convex on both the flank and the umbilical wall. The sculpture is weakened on the flanks of the living chamber. No reliable observations of the bundling habit can, therefore, be made on the holotype. However, it is possible to assume the presence of bidichotomous bundles with some solitary intercalated secondaries. Some 13 bullae were estimated to be present. Several other specimens, in which the living chamber is preserved, are closely similar to the holotype. The other two previously figured specimens (Kemper, 1963, Pl. 36, fig. 3 = BGR, kv 47 and Kemper, 1976, Pl. 30, fig. 2 = BGR, kv 66) belong to the conservative form of the species. In the specimen BGR, kv 66 reproduced herein on Pl. 2, fig. 1 the last preserved whorl is almost entirely a living chamber and everything indicates that it also represents the adult growth stage. The beginning of the last whorl of this specimen is covered by a characteristically bidichotomous sculpture. The last whorl is ornamented by 16 bullae. The sculpture disappears on the last quarter of the last whorl. This specimen exhibits less distinct forward bends of the ribs on the flanks as compared with the holotype. The weakening of the sculpture, which is restricted to the flanks, begins here at the beginning of the living chamber. It begins considerably earlier in specimen BGR, kv 47.

Affinities and differences. The specimen figured in this paper (BGR, kv 66; Pl. 2, fig. 1) is a form transitional to the ancestral group of *Propolyptychites quadrifidus* (Koenen). Therefore, it exhibits only feebly the characteristics of the *bentheimensis* trend. Typical representatives of the species are morphologically distinctive and cannot be confused with any other species of Polyptychitinae.

Genus *Polyptychites* Pavlow 1892

Type species. Polyptychites polyptychus (Keyserling 1846).

Diagnosis. A polyptychitinid genus combining the presence of two to more commonly three (in evolutionarily advanced species only) auxiliary lobes with a total absence of constrictions and the presence of an exclusively tripartitously ribbed sculptural stage on early or intermediate whorls. The whorl is mostly regularly arched and moderately sturdy (not much wider than high) in all growth stages but is relatively more slender in the early growth stages. The shell may acquire a sphaeroidal to barrel-like, acute-shouldered (i.e. *Euryptychites*-like) cross-section in late growth stages of some species.

Discussion. The genus is one of those ammonite taxa which are difficult to interpret. The reasons are:

1) The previously and in part still poorly understood sequence of species;
2) Prevalence of living chambers or juvenile whorls among the type specimens of its species;
3) Extreme splitting accompanied by the lack of diagnoses and indications of characteristic differences of erected species practiced by Koenen (1902, 1909);
4) Great intraspecific variability of some species; and
5) Existence of regional evolutionary lineages, which arose following interregional migrations of some species outside their normal ranges.

These difficulties are augmented by the problematic nature of the type species (see under its description). The specimen figured by Wright (in Arkell et al., 1957, p. L348, Text-fig. 457-2) and Drustchits & Bodylevsky (in Khimiashvili et al., 1958, p. 93; Pl. XLII, fig. 2; Figure 77a) is not *P. polyptychus* (Keyserling). This well described and figured specimen (Pavlow, in Pavlow and Lamplugh 1892, p. 477-78; Pl. XV, fig. 2a-2c) is, instead, a typical representative of the *Polyptychites keyserlingi* species group, which includes the very core of the genus *Polyptychites* in its traditional European interpretation.

No subgenera are recognized for the time being in *Polyptychites* following the exclusion of the genus *Siberiptychites* Kemper and Jeletzky 1977 from that genus as proposed in the second part of this paper.

The writers are fully aware of the fact that *Polyptychites* as restricted herein continues to comprise several evolutionary lineages (or offshoots from its main stem) which are (with some exceptions) confined to the boreal basins of Europe. It may be necessary to separate some of these lineages as subgenera of *Polyptychites*. However, the writers prefer to differentiate them as groups of species or evolutionary lineages of the genus *Polyptychites* for the time being. Their characteristic features will be discussed below.

The external suture lines of *Polyptychites* and *Dichotomites* Koenen 1909 were comprehensively discussed by Pavlow (in Pavlow & Lamplugh, 1892, p. 476). This description, which is still valid for the genus *Polyptychites* in the writers' opinion, is: "Cloisons assez découpées; outre le lobe siphonal et les deux latéraux, on observe le plus souvent deux lobes auxiliaires, rarement trois. Selles subdivisées en deux branches inégales; les sommets de la selle externe et des deux latérales touchent la ligne radiale ou ne montent que faiblement. Les selles auxiliaires s'abaissent un peu vers la suture."

However, this suture line is only diagnostic of the genus if used in combination with other morphological features, such as the apparently total absence of constrictions in all growth stages and a characteristic ontogenetic sequence of sculptural stages. The latter is characterized by the persistence of a predominantly trivirgatitpartitous (=bimonotomous of Kemper, 1978, p. 189, Figure 1) mode of bundling on all early and intermediate whorls preceding those advanced to adult whorls ornamented largely or entirely by bidichotomous, quadrivirgatitpartitous, polyptychous and fasciculate rib bundles.

The simple dichotomous and the second trivirgatitpartitous sculptural stages characteristically inserted between the above mentioned stages in *Siberiptychites* are totally unknown in *Polyptychites*.

Because of these morphological distinctions combined with the prevalent restriction of *Polyptychites* and *Siberiptychites* to different regions of the Boreal Realm and the apparent derivation of *Siberiptychites* from another largely North Siberian genus *Bodylevskites* Klimova 1978, the two genera do not appear to be immediately genetically related.

1st Group: *Polyptychites michalskii* (Bogoslovsky) — *P. oerlinghusanus* (Weerth)

Summary: Small to moderately large species with relatively refined sculpture in the intermediate growth stages. Primary ribs are slender and high. Bullae are fine and make their first appearance late in the ontogeny — commonly on the living chamber. The rather constant bundling habit consists, at least on the exposed whorls, of trivigatitpartitous bundles. Only subordinate deviations from this habit caused by insertion of supplementary elements have been observed.

2nd Group: *Polyptychites keyserlingi* (Neumayr & Uhlig)

Summary: Species that have a broadly rounded venter and predominantly thick whorls with strongly convex flanks. Strongly and typically developed bullae develop out of the primary ribs already early in the ontogeny. The sculpture of middle growth stages is trivirgatitpartitous. On the penultimate whorl the number of secondary ribs increases to 5-6 and the bundling becomes bidichotomous to polyptychous only in some exceptional to rare bundles.

2a. Subgroup of *Polyptychites pavlowi* Koenen — *P. lamplughi* Pavlow

Summary: Moderately large species with a wide and relatively shallow umbilicus and tube-like whorls. The flanks are strongly convex and broadly rounded (a Roman arch) on the venter. The width of whorls increases only slowly in the course of ontogeny. In the adult state it decreases rather than increases, relatively speaking. The sculpture is coarse with markedly elevated bullae. In addition to the species mentioned in its title, this subgroup includes also *P. brancoi* (Neumayr & Uhlig).

2b. Subgroup of *Polyptychites keyserlingi* (Neumayr and Uhlig).

Summary: This subgroup consists of *P. keyserlingi* alone, which is characterized by a great variability. It is a moderately large species with thick whorls. The tendency of the progressive variants to a strong increase of the width of the whorl in the adult growth stage is especially characteristic of the species. The flanks are strongly convex and the venter broadly rounded (Roman arch). The sculpture is coarse. The sculpture of the penultimate whorl is dominated by quasiquadrivirgatitpartitous bundling habit. Some bundles with 5-6 secondary ribs appear in the progressive variants only.

2c. Subgroup of *Polyptychites ascendens* Koenen.

Summary: Small *Polyptychites* species characterized by only a slight increase in whorl width in the course of ontogeny and a refined sculpture combined with well developed bullae. The bundling habit is similar to that of the *keyserlingi*-Subgroup.

3. Group of *P. hapkei* n. sp.

Summary: Large species with a coarse sculpture of *orbitatus*-type, which is dominated by tridichotomous rib bundles; suture line mostly with three auxiliary lobes. There is a tendency for the development of wide, euryptychitoid whorls, especially in the adult growth stage. This is probably the rootstock of the "younger *Euryptychites*" (= *Hollwediceras*). The doubtful species *P. sphaeroidalis* Koenen and *P. triplodiptychus* Pavlow are here included in this group.

4th Group: *Polyptychites multicostatus* Koenen.

Summary: Species with only feebly convex flanks and narrowly rounded venter. Sculpture is refined and dense. The rib bundles on the penultimate whorl include at least 5 and commonly more supplementary ribs. This is the rootstock of the younger, central European *Polyptychites* species.

4a. Subgroup of *P. multicostatus* Koenen and *P. clarkei* Koenen.

Summary: The bundling habit, which is essentially of *keyserlingi*-type, remains conservative and variable. However, the sculpture is considerably more refined and denser. The points of subdivision of primary ribs are situated rather adumbilically in one group of variants. Another group of variants exhibits a tendency for bundles to differentiate into secondary and tertiary ribs.

4b. Subgroup of *P. orbitatus* Koenen (includes also *P. saxonicus* n. sp., *P. tethyale* n. sp., *P. sublatissimus* Spath).

Summary: Large species with refined and dense sculpture, which clearly belongs to the *orbitatus*-type of bundling at least at one of the ontogenetic stages. The *orbitatus*-type bundling is characterized by a clear differentiation into secondary and tertiary ribs. Subdivision of ribs is rather regular and results in the appearance of tridichotomous bundles.

Polyptychites polyptychus (Keyserling 1846)

Discussion. *P. polyptychus* is the type species of the genus *Polyptychites*. As happens so often, it is the type species that is of a most problematic nature. Keyserling (1846, Pl. 21, fig. 1-3) provided drawings of two ammonites, one from the Pechora region (River Ishma) and another one (collected by von Middendorff) from the Olenek River in North Siberia. The latter was figured in Pl. 21, fig. 2 of Keyserling's work. The suture line reproduced in his fig. 3 is also from that specimen. The correspondence of the illustrations of both specimens with the originals cannot be determined. These originals must have been available to Pavlow as he notes that the drawings of them provided by Keyserling (l. cit.) are strongly reduced and that his reproduction of their sculpture is incorrect (Pavlow, in Pavlow and Lamplugh, 1892, p. 478). Also Keyserling (1846, p. 328, above) himself admits that his drawings do not reproduce correctly the sculpture of the originals.

Pavlow, in Pavlow and Lamplugh (1892, Pl. 15, figs. 2a, b) figured at the same time a specimen from Speeton under the same name, which was subsequently utilized (especially in the recent Treatises, such as the Treatise on Invertebrate Paleontology, Osnovy) to typify *P. polyptychus*.

The writers studied a plaster cast of the Speeton specimen figured by Pavlow (l. cit.) the original of which is preserved in the York Museum. This well preserved specimen is distinguished by the low cross-section of its whorl and a wide umbilicus. In these features, and in its sculpture and suture line as well, it agrees well with the Northwest German representatives of *Polyptychites pavlowi* Koenen. It differs from them only in the broad rounding of its oralmost preserved halfwhorl and its somewhat greater width. Contrary to Pavlow (l. cit.), it can be assumed that at least the oralmost quarter of the last preserved whorl is occupied by the adult living chamber. As the minor distinctions of our specimen from the typical morphology of *P. pavlowi* can be ascribed to the aberrant variation of its adult growth stage, this alleged Speeton representative of *P. polyptychus* may be referred to *P. pavlowi*. Therefore, it cannot serve as an example of *P. polyptychus*. The unfortunate publication of a specimen that does not belong to this species under the name of *P. polyptychus* and, even more, its inclusion as such in the Treatises has created an entirely false idea about the morphology of the type species of the genus *Polyptychites*.

According to the inquiries made by E. Kemper in the Chernyshev Museum, Leningrad, during his 1982 visit there, the originals of Keyserling (1846) are lost. No ammonites that could be identified as *P. polyptychus* were ever again found in the Pechora Province, that is in one of its type-areas. However, the other type-area — Northern Siberia — has subsequently yielded specimens that were considered to belong to *P. polyptychus* by the Soviet paleontologists who had worked in that region (Dr. N.I. Shulgina, verbal communiation to Dr. E. Kemper in 1982). One of these specimens could and should be designated as its neotype. The clarification of this problem is beyond the scope of this paper.

It is important to point out in this connection that *P. polyptychus* is actually a late Valanginian species, as was always pointed out in the Soviet literature. It first appears there later than does the genus *Dichotomites*. Kemper now recognizes *P. polyptychus* (Keyserling) in Northwest Germany, where it is represented by a small ammonite previously assigned to *Dichotomites crassus* (Kemper, 1978, Pl. 7, fig. 2). This specimen resembles strongly those examined from North Siberia that were interpreted as *P. polyptychus* by the Soviet paleontologists. E. Kemper also reassigns the holotype of "*Dichotomites*" *crassus* Kemper 1978, and therefore the species, to *Polyptychites*. *P. crassus* belongs to that widely umbilicated species group that occasionally occurs in North Siberia in association with *P. polyptychus* and the oldest known *Dichotomites*. This fauna is also comparable to that of the lower *Polyptychites*-Bed of Mangyshlak (Luppov, Bogdanova and Lobachova, 1979), that is already of an upper Valanginian age.

The finds of this young, late Valanginian *P. polyptychus* species group are very scant in Northwest Germany, and nonexistent in the Sverdrup Basin. A further discussion of the subject is, therefore, beyond the scope of this paper.

Polyptychites michalskii (Bogoslovsky 1902)

Pl. 2, fig. 2

1892	*Olcostephanus (Polyptychites) beani* Pavlow in Pavlow and Lamplugh, p. 481, 482 (pars), Pl. 8, figs. 11a, b.
*1902	*Olcostephanus michalskii* Bogoslovsky, p. 133, 134, Pl. 15, figs. 1a, 1b; 2a, b; 3a, b(?); 5a, b; 7 (?non cf. *michalskii* var: Pl. 15, figs. 6a, b, c)
?1902	*Olcostephanus michalskii* var. *tuberculata* Bogoslovsky, p. 135, Pl. 15, figs. 4a, 4b.
1958	*Polyptychites michalskii* Luppov and Drustchits (in Khimiashvili et al.), p. 93, Pl. 47, figs. 1a, b.
non 1967	*Polyptychites* aff. *michalskii* Bodylevsky, p. 111, Pl. 9, figs. 4a, b.
1968	*Polyptychites michalskii* Kemper, p. 31, Pl. 22, fig. 5 (non Pl. 25, fig. 5a, b).
1976	*Polyptychites* juv. indet. Kemper, p. 34, Pl. 22, fig. 5.

(There are many quotations without figures in the Russian literature, which cannot be definitively interpreted).

Holotype. Bodylevsky (1967, p. 111) has selected the specimen figured by Bogoslovsky (1902, Pl. 15, fig. 2a, b) from Valanginian rocks on Pechora River, USSR as the lectotype of our species. Exact stratigraphic level unknown.

Diagnosis. Presumably small to at the most medium-sized but relatively thick species of the genus with slender but nevertheless high and sharp ribs. Primary ribs numerous, slender and sharp. The slight bullate ribs appear only in adulthood. The bundling habit is trivirgatitpartitous in the intermediate growth stages. Whorls are broad. The adult venter is feebly convex rather than broadly arched and tends to be slightly flattened.

Measurements. See data provided by Bogoslovsky, 1902, p. 133.

Description. Only one small and juvenile representative from the *Platylenticeras*-Beds (lower lower Valanginian) of Suddendorf (Pl. 2, fig. 2, BGR, kv 261) has been found in Northwest Germany. It probably belongs to the oldest and morphologically conservative representatives of the species and differs from its more typical representatives found in the Pechora Region in a relatively wider umbilicus and only moderately thick whorls. At the same time it exhibits especially clearly the typical ribbing habit of the species. The primary elements form sharp rib stems (21 of them on the last preserved whorl), which split into trivirgatitpartitous bundles closely above the middle of the flank. The bullae have not yet appeared.

The suture line of the German specimen is not known. That of the Russian representatives was stated to be identical with the suture of *P. polyptychus* (Keyserling) (Bogoslovsky, 1902, p. 134).

The specimens from Pechora Region figured by Bogoslovsky (1902, Pl. 15) are more progressive morphologically. Their whorls are thicker and exhibit a tendency to a flattening of the venter. This results in a slightly trapezoidal whorl section. Furthermore, their umbilicus is more narrow. The slender primary ribs acquire the shape of refined bullae at whorl diameters of 25-30 mm. At the same time the point of subdivision of primary ribs migrates from the middle of the flank markedly toward the umbilicus. Further details can be perused in the detailed description provided by Bogoslovsky (1902).

Affinities and differences. *P. michalskii* is, like *P. polyptychus*, a *Polyptychites* that is commonly cited in the U.S.S.R.; there it is considered to be the index fossil of the late early Valanginian. It is impossible to decide without a study of a more numerous Russian material whether the strongly bullate forms (see Bogoslovsky, 1902, Pl. 15, figs. 4a, 4b) are variants of *P. michalskii* or should be assigned to *P. keyserlingi*. However, their interpretation as variants of *P. michalskii* that are homeomorphs of *P. keyserlingi* appears more likely. Diagnostic of *P. michalskii* is its refined sculpture, which possesses at the most suggestions of bullae, in combination with small and relatively thick whorls.

P. michalskii is probably closely related to *P. ramulicosta* Pavlow (see below). *P. michalskii* cannot be confused with *P. oerlinghusanus* principally because of its considerably thicker whorls.

P. michalskii probably arose from the early Polyptychitinae of Northwest Europe, judging by the appearance of the specimen figured here (Pl. 2, fig. 2). It must have migrated subsequently into the sedimentary basins of Eastern Europe where the principal phase of its development took place. In central and western Europe it must have been rapidly expelled by *Polyptychites* of the *pavlowi-keyserlingi* species group.

In eastern Europe and North Siberia, *P. michalskii* forms part of a lineage which possibly evolved into the younger species (e.g. *P. polyptychus*, *P. crassus*), in which the trivirgatitpartitous rib bundles extend also into the intermediate growth stages.

Polyptychites oerlinghusanus (Weerth, 1884)

Pl. 4, fig. 6; Pl. 6, fig. 5; Pl. 7, fig. 3; Pl. 24, fig. 1,
Figures 18a, 18b.

1884 *Ammonites (Olcostephanus) Oerlinghusanus* Weerth, p. 18, Pl. 4, figs. 4a, b (non 3a, b).
non 1914 *Polyptychites oerlinghusanus* Pavlow, p. 23, 24, Pl. 4, fig. 5a, b.

Lectotype. The specimen reproduced by Weerth (1884, Pl. 4, fig. 4a, b) is selected herewith as lectotype of the species. This specimen is probably lost. However, an unfigured topotype is present in the Weerth collection in the Lippische Landesmuseum, Detmold.

Locus typicus. Toensberg near Oerlinghausen.

Stratum typicum. Osning sandstone. Exact age and correlation unknown. The specimens figured in this paper are derived from the lower *Polyptychites*-Beds of Bueckeburg-Jetenburg (lower Valanginian).

Material. 16 specimens from the localities Oerlinghausen, Bueckeburg-Jetenburg and Lindhorst. 2 of them are in Detmold and 14 in BGR collections, Hannover.

Diagnosis. Small and very slender species of the genus combining slender but low whorls with a wide umbilicus. Primary ribs slender and high. Only in the adult growth stage do they become slightly bullate. Very simple adult external suture has three auxiliary lobes, the first of which is situated on the lower flank.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
BGR. kv 262	38	13(34)	11(27)	13(34)	12	15
BGR. kv 263	41	15(33)	12(30)	25(33)	11	15
BGR. kv 264	42	13(31)	13(31)	16(38)	12	16

Description. As Weerth (1884) has lumped rather different ammonites under the name of *P. oerlinghusanus* it is necessary to select a lectotype and to provide a new description of the species in this paper. The species is small and its shell diameter apparently barely reaches 60 mm. As is evident from the table of measurements, its whorls are slender and at the same time low. The shell is almost moderately evolute with the later whorls only insignificantly (about 50 per cent) enclosing the earlier whorls. The umbilicus is shallow and moderately wide (about 33 per cent). The living chamber reaches barely the length of one whorl.

The flanks are only feebly convex. The largest width of the whorl is situated slightly above the umbilical shoulder which results in the cross-section being approximately oval. The umbilical shoulders are broadly rounded and grade into low and mostly convex umbilical walls. The umbilical wall may be somewhat more steep on the penultimate whorl.

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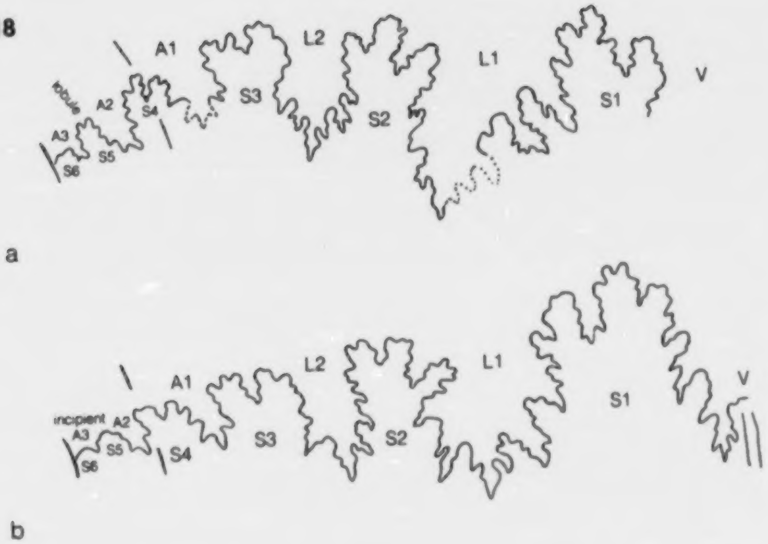
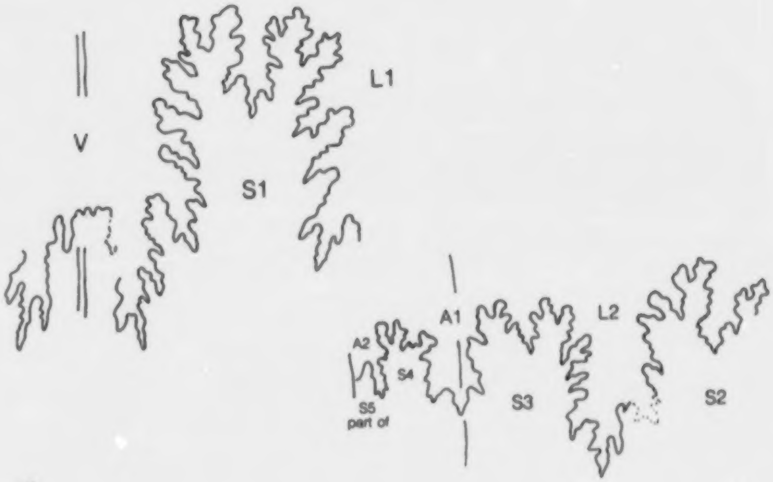


Figures 18a, 18b, 19. Adult external suture lines of *Polyptychites oerlinghusanus* (Weerth, 1884) and *P. pavlowi* Koenen, 1902. **18a**. *P. oerlinghusanus*, specimen BGR kv 335 from Bueckeburg-Jetenburg, Northwest Germany. Older *Polyptychites*-Beds, early Valanginian. The terminal suture before the ?adult living chamber at the whorl height of about 13 mm, x 6 (approx.). **18b**. *P. oerlinghusanus*, specimen BGR kv 264. The same locality and age as for the specimen kv 335. Adult suture exposed on the presumably adult penultimate whorl at the whorl height (wh) of about 12.5 mm, x 6.5 (approx.). 19. *P. pavlowi*, specimen BGR kv 61 reproduced in Pl. 5, fig. 1A (see its explanation for further details). Two incomplete adult sutures visible respectively at the whorl heights (wh) of about 22 mm (the ventral part, x 7.9) and 26 mm (lateral and the umbilical parts, x 4.1).



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Several examples of presumably adult external suture lines are known. (e.g. BGR, kv 264 and 335; Figures 18a, 18b). They are characteristically simple with short and stubby lobes either shallowly and simply denticulated (i.e. lateral lobes) or only notched (i.e. auxiliary lobes). The width of the first and second lateral saddles is subequal to that of the preceding lobes while that of the third to fifth lateral saddles is only slightly greater than that of the preceding lobes.

The asymmetrically trifid first lateral lobe is only slightly shorter than and comparably wide with the ventral lobe. However, it is twice as long and twice as wide as the second lateral lobe, which is situated somewhat beyond (i.e. adumbilically of) mid-flank. This second lateral lobe is almost symmetrically trifid but its terminal prongs are very short and simple (almost simple notches).

The length and width of the first auxiliary lobe comprise somewhat less than one-half of those of the second lateral lobe. This auxiliary lobe is situated on the flank just before the umbilical shoulder. It tapers adapically toward a shallowly notched but distinctly trifid tip. Its flanks are but slightly notched.

The second auxiliary lobe occupies the outer half of the narrow umbilical wall. It is only slightly smaller than the first auxiliary lobe, tapers apicalward all the way to its slightly notched, indistinctly trifid tip and is only slightly notched on the flanks.

The third auxiliary lobe is situated at the boundary between the middle and the inner thirds of the umbilical wall. It is a tiny, simple, subtriangular-shaped but round-tipped structure in BGR, kv 264 (Figure 18b). The fifth saddle separating it from the second auxiliary lobe is almost simple. However, it is a relatively much larger, distinctly albeit simply notched structure in BGR, kv 335 (Figure 18a) where the fifth saddle is subdivided in two by a small, tack-like lobule.

The inner third of the umbilical wall is occupied by the relatively widened, presumably almost completely exposed sixth lateral saddle, which is not appreciably notched in the material studied. No part of the fourth auxiliary lobe is visible in any of the examples studied.

The lateral part of the suture line is markedly (at 15 to 20 degrees in relation to the corresponding radius) ascendant while its whole auxiliary part is subradially to slightly descendantly oriented. The two parts meet at an angle within the third lateral saddle. All adult sutures are well spaced. Even the somewhat approximated oralmost two or three suture lines do not begin to touch.

The adult external suture line of *P. oerlinghusanus* is peculiar in combining such morphologically and presumably evolutionarily conservative features as:

1. The short and stubby, shallowly and simply denticulated to only notched morphology of its lobes; and

2. The narrow, simply denticulated morphology of its saddles; with other features that are morphologically and presumably evolutionarily advanced. The latter include the presence of three auxiliary lobes, the positioning of both lateral lobes and the first auxiliary lobe on the flank and the markedly ascendant orientation of the lateral part of the suture line combined with a mostly subradial orientation of its auxiliary part. This suture is considered to be a specialized derivative of the conservative polyptychitinid suture line (typified by that of *P. pavlowi*; Figure 19) that is not ancestral to any of the younger variants of the advanced polyptychitinid sutures.

The sculpture is fine in the juvenile growth stage and becomes coarser in the adult state. The primary ribs are slender but high and sharp. Only on the living chamber do they acquire a bullate appearance because of a more or less pronounced elevation. However, they remain slender and persist adventrally as primary ribs as their subdivision into the secondary ribs takes place only in the proximity of the midflank in the adult growth stage. There are about 22 primary ribs on the penultimate whorl. The number of primaries decreases somewhat (about 20 per whorl) on the living chamber. The primary ribs are oriented approximately radially in the early growth stages. They become comma-like on the penultimate whorl but this bend is lost again on the last whorl. The primary ribs and bullae extend for some distance onto the umbilical wall.

The ribbing habit of the early growth stages remains unknown. However, there are some indications of the presence of a stage with bidichotomous rib bundles. A trivirgatitpartitous ribbing habit is prevalent on the last exposed whorls (i.e. penultimate and ultimate). The stems of primary ribs or bullae split in two secondary ribs, of which only the posterior splits in two again. The sculpture of the living chamber is more irregular, as the anterior secondary ribs of its bundles are displaced relatively more adventrally. This results in the formation of trivirgatitpartitous rib bundles (Kemper, 1978, p. 189, Fig. 1). The intercostal spaces become wider at the same time. In the adult state the secondaries may form slight forward bends on the ventral shoulders and venter. The basically trivirgatitpartitous mode of bundling is present fairly constantly. Only seldom does it become more irregular because of a suppression or an addition of a tertiary rib.

Affinities and differences. The species is an early but specialized offshoot of *Polyptychites* known only from the Lower Saxony Basin. The similarly large, early growth stages of *P. pavlowi* Koenen may have a generally similar appearance. However, they are wider and their whorls are more broadly rounded, instead of oval. Furthermore, *P. pavlowi* is several times larger than our species and has a more conservative adult external suture line with only two auxiliary lobes. *P. michalskii* Bogoslovsky is somewhat similar in the lateral aspect. However, its cross-section is trapezoidally shaped and much wider and its external suture line is said to be exactly like that of *P. polyptychus*. *P. oerlinghusanus* cannot be confused with any other *Polyptychites* species.

Polyptychites pavlowi Koenen 1902

Pl. 4, figs. 2, 3, 4, 5; Pl. 5, figs. 1, 2; Pl. 10, fig. 2; Pl. 27, fig. 5; Pl. 28, fig. 5; Figures 19, 20.

1892	*Olcostephanus (Polyptychites) polyptychus* Pavlow in Pavlow and Lamplugh, p. 477-478, Pl. XV (VIII), fig. 2.
*1902	*Polyptychites keyserlingi* var. *pavlowi* Koenen, p. 134-136, Pl. 1, figs. 1-3.
1902	*Polyptychites euomphalus* Koenen, p. 116-118, Pl. 55, figs. 5a, b.
non? 1902	*Polyptychites* juv. aff. *euomphalus* Koenen, p. 119, Pl. 55, figs. 8a, b, 11a, b.
1906	*Olcostephanus (Polyptychites)* aff. *Beani* Danford, Pl. 11, figs. 2, 2a.
1909	*Polyptychites obtusus* Koenen, p. 73, 74, Pl. 11, figs. 1, 3.
?1909	*Polyptychites depressus* Koenen, p. 53-55, Pl. 16, figs. 1, 2.
non 1909	*Polyptychites euomphalus* Koenen, p. 82-83, Pl. 33, figs. 1, 2.
1924	*Polyptychites* aff. *subrectangulatus* (= "aff. *beani*" in Danford 1906, Pl. 11, figs. 2, 2a) Spath, p. 75.
1957	*Polyptychites polyptychus* Wright, in Arkell et al, p. L349, fig. 457-2a-2c.
1958	*Polyptychites polyptychus* Drustchits and Bodylevsky (in Khimiashvili et al., p. 93; Pl. XLII, fig. 2; Figure 77a).
1973	*Polyptychites euomphalus* Kemper, p. 335.
1976	*Polyptychites euomphalus* Kemper, p. 38, Table 6.
1977	*Polyptychites euomphalus* Kemper, Fig. 2.

1978 *Polyptychites euomphalus* Kemper, Ernst, and Thiermann, Table 1.

Holotype. The specimen reproduced by Koenen 1902, Pl. 1, figs. 1-3.

Locus typicus. Osterwald.

Stratum typicum. Uncertain but very probably lower to middle lower Valanginian.

Material. Some 80 specimens from the lower *Polyptychites*-Beds (middle lower Valanginian) of the localities Bueckeburg-Jetenburg and Lindhorst.

Diagnosis. Medium-sized species of the genus with a wide umbilicus and low but at the same time slender whorls. The thickness and height of the whorls increase only very slowly in the course of ontogeny. The sculpture is variable. The adult external suture line is simple and has only two auxiliary lobes.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
BGR, kv 63	81	24(30)	25(31)	33(40)	31	36
BGR, kv 59	85	28(33)	25(29)	31(37)	25	33
BGR, kv 60	93	31(33)	26(31)	35(38)	—	—
BGR, kv 61	75	24(32)	23(31)	28(37)	—	32
BGR, kv 65	66	23(35)	19(29)	23(35)	—	—
BGR, kv 265(juv.)	46	15(33)	13(28)	18(39)	15	19

Description. The holotype (Koenen 1902, Pl. 1, fig. 1-3) is poorly preserved and its figure is difficult to interpret because of strong reduction. It is obviously a large-sized, morphologically extreme variant of the species. Morphological details, except for the number of bullae, are not visible and one has to use the description provided by Koenen (1902) for that end.

The abundant material on which this study is based, permits for the first time a review of this important species which is ancestral to other species of *Polyptychites*. Together with *P. keyserlingi*, it includes the bulk of the *Polyptychites* forms found in Northwest Germany. The species exhibits a great range of variation in many of its morphological features, which reflects its evolutionarily central position. It also exhibits transitional forms to the species derived from it. The species is interpreted here in a very broad sense. One could feel inclined to attempt a further subdivision.

The shell is broadly umbilicate (about 33 per cent). It is, furthermore, characterized by only a small increase in the thickness and height of the whorl. The whorls are, therefore, slender (Figures 20a, 20b). As the succeeding whorls enclose the preceding whorls only slightly (± 67%), the umbilicus is step-like shaped and shallow. The whorl section varies from a median type with regularly arched (Roman arch-like; e.g. BGR, kv 63) venter to one extreme type with a slender and narrowly arched venter (BGR, kv 59) and another in which the whorls have almost parallel flanks (BGR, kv 60 and 61). The umbilical shoulder is broadly rounded, particularly in the early stages. The umbilical wall is rather gently inclined (it forms a 60 to 70° angle with the plane of shell's symmetry) and slightly convex. The living chamber is about one whorl long.

The advanced to adult external suture lines, which are best exposed on adult penultimate whorls of the specimens BGR, kv 61 and BGR, kv 65 (Pl. 5, fig. 1A; Figure 19), are of the same general type as those of *Polyptychites oerlinghusanus* where the shape and spacing of their elements are concerned. They are also similarly oriented. The same is true of the adult external suture line of the holotype of *P. pavlowi* as drawn by Koenen (1902, Pl. 1, figs. 1, 3). However, all these suture lines have only two auxiliaries and so are distinctly more conservative than those of *P. oerlinghusanus*. Other, less significant differences include:

1. A somewhat more complex and deeper denticulation of all lobes and saddles;

2. A distinct constriction of topmost parts of the lateral lobes and the first auxiliary lobe;

3. A prevalent positioning of the first auxiliary lobe either directly on the umbilical shoulder or already on its inner side; and

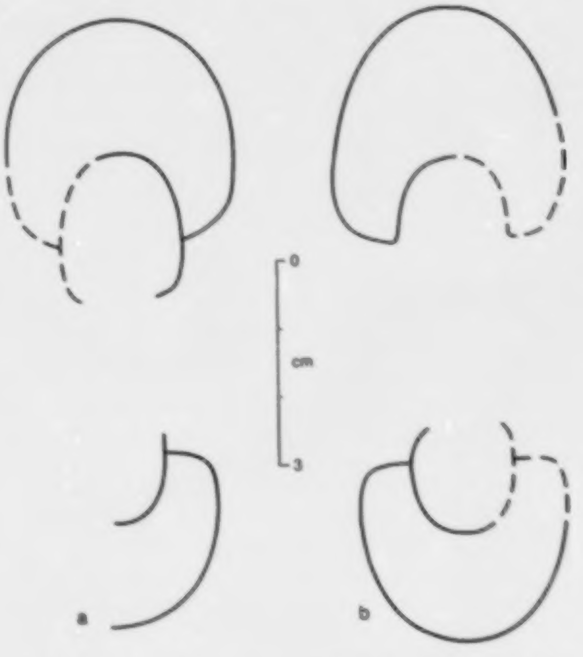


Figure 20. Cross-sections of *Polyptychites pavlowi* Koenen, 1902. Note the linear scale. **a.** Specimen BGR kv 314 from Bueckeburg-Jetenburg, Northwest Germany. Lower *Polyptychites*-Beds, mid-early Valanginian. **b.** Specimen BGR kv 315 from the same locality and of the same age as the specimen BGR kv 314.

4. A relatively greater size (especially width) of the second auxiliary lobe frequently (except in the holotype) coupled with its positioning just at the umbilical seam.

The sculpture is also variable. Variants with broadly rounded whorl section, which connect the species with *P. ascendens*, have a relatively refined and dense sculpture (e.g. specimens BGR, kv 59 and kv 265 reproduced in Pl. 4, fig. 3A and Pl. 10, fig. 2 respectively and the unfigured specimen BGR, kv 63). The primary ribs remain slender and high to a shell diameter of about 40 mm, then gradually become bullate. In the specimens BGR, kv 59 (Pl. 4, fig. 3) and kv 63, the penultimate whorl carries 22 primary ribs while the last whorl carries 20 bullae. The primary ribs and bullae are incurved forward on the umbilical wall. They disappear in the middle of the umbilical wall.

The sculpture is very fine and dense to a shell diameter of about 20 mm (Pl. 4, fig. 4). In this interval it consists of alternations of trivirgatitpartitous and trifasciculate rib bundles with rarely single intercalated ribs. At shell diameters exceeding 25 mm it consists of high and considerably more distant ribs, which form trivirgatitpartitous bundles. Solitary dichotomous intercalated elements may intervene between the bundles (e.g. BGR, kv 265; Pl. 10, fig. 2). At shell diameters of 45-50 mm appear additional ribs, so that the penultimate whorl is dominated by bundles with 4 to 5 secondary ribs. Because of an addition of a tertiary rib in front of the trifurcate bundle, there reappear, in part, quasibidichotomous bundles (BGR, kv 63). However, a polyptychoid bundling habit can also arise at this growth stage (BGR, kv 59, Pl. 4, fig. 3; BGR, kv 78, Pl. 4, fig. 2). On the last preserved whorls, which represent in part the adult living chamber, occurs a reduction of the number of ribs. For example, the ribbing habit of BGR, kv 63 returns, in the essence, to a trivirgatitpartitous style. The ornament of the last whorl of the specimen BGR, kv 59 (Pl. 4, fig. 3) is very irregular. It consists of an alternation of trivirgatitpartitous and quadrivirgatitpartitous bundles with quasibidichotomous bundles and intercalated bidichotomous ribs.

The coarser and less dense sculpture occurs mainly in those specimens in which the convexity of the flanks is reduced, at least in the advanced growth stages (e.g. BGR, kv 60 and kv 61 reproduced in Pl. 5, fig. 1). The primary ribs are high and sharp, becoming thickened and accordingly bullate only at shell diameters of 40 to 50 mm. The number of these primary elements characteristically comprises about 16 on the penultimate and ultimate whorls. The ontogeny of this sculptural type is rather poorly understood. Its intermediate stages are again dominated by trivirgatitpartitous rib bundles. A short stage with quadrivirgatitpartitous and polyptychous bundles is then followed by an irregularly ribbed adult growth stage which has a reduced number of ribs. The latter stage consists of quasibidichotomous and trivirgatitpartitous bundles with intercalated single and dichotomous ribs.

An extreme variant of the species with a relatively greater number of ribs per bundle was figured by Pavlow (in Pavlow and Lamplugh, 1892, Pl. XV, fig. 2a) as *P. polyptychus* Keyserling (see p. 46 for further details).

Affinities and differences. *P. pavlowi* evolved out of the stock of *Propolyptychites quadrifidus* and is itself the rootstock of *Polyptychites*. It is connected by transitional forms to *P. brancoi*, *P. lamplughi*, *P. keyserlingi* and *P. ascendens* which have developed from it (Figure 11). *P. pavlowi* differs from these species mainly in its more slender whorls with only a very slow increase in their width and height during ontogeny. These distinctive features are combined with a wide umbilicus. *P. brancoi*, which possesses a similarly wide umbilicus and is relatively slender, differs from *P. pavlowi*, among other things, in a considerably coarser sculpture (approximately 11 coarse bullae per whorl in the adult growth stage). *P. ascendens* differs, in particular, in its more narrow umbilicus. Furthermore, it differs from the more finely ribbed representatives of *P. pavlowi* in its thicker whorls. However, the two are connected by transitions (Pl. 10, fig. 2).

The species is known only from Northwest Germany and Eastern England (Speeton). It is not possible to determine definitively the specimen figured by Pictet and Campiche (1858-60, Pl. 41, figs. 1a, b), as the drawing is presumed to be not true to the nature. Should the specimen belong to *P. pavlowi*, its geographical range would extend into Tethys.

Polyptychites brancoi (Neumayr & Uhlig 1881)

Figures 21a, 21b

*1881	*Olcostephanus Brancoi* Neumayr and Uhlig, p. 156, 157, Pl. 26, figs. 1, 1a.
1892	*Olcostephanus (Polyptychites) keyserlingi* Pavlow, in Pavlow and Lamplugh, p. 478, 479, (pars), Pl. 15, figs. 5a-5c.
1902	*Olcostephanus neritzensis* Bogoslovsky, p. 137, Pl. 14, figs. 3-5.
1902	*Polyptychites Brancoi* Koenen, p. 136, 137, Pl. 50, figs. 4, 5 (non Pl. 55, figs. 9a, b).
1909	*Polyptychites karpinskii* Koenen, p. 33, 34, Pl. 13, figs. 1, 4.
1909	*Polyptychites schmidti* Koenen, p. 45, 46, Pl. 9, figs. 3, 4.
1909	*Polyptychites asper* Koenen, p. 39, 40, Pl. 15, figs. 2, 3.
1909	*Polyptychites lessingi* Koenen, p. 41, 42, Pl. 17, figs. 1, 2.
1909	*Polyptychites lamplughi* Koenen, p. 46, 47, Pl. 19, figs. 1, 2.
1909	*Polyptychites lahuseni* Koenen, p. 48, 49, Pl. 20, figs. 2, 4.
1909	*Polyptychites stillei* Koenen, p. 61, 62, Pl. 24, figs. 1-4.
1909	*Polyptychites euomphalus* Koenen, p. 82, 83, Pl. 33, figs.1, 2.

Holotype. Specimen figured by Neumayr and Uhlig, 1881, Pl. 26, figs. 1, 1a is the holotype of *P. brancoi* by monotypy. It was reproduced by Koenen (1902, Pl. 50, figs. 4, 5).

Locus typicus. Neustadt at Ruebenberge.

Stratum typicum. Unknown. According to the finds of *P. brancoi* at other localities, it occurs in the lower *Polyptychites* Beds (middle part of the lower Valanginian).

Material. 13 moderately well to poorly preserved specimens from the localities Bueckeburg-Jetenburg and Lindhorst.

Diagnosis. Medium-sized species of *Polyptychites* which is relatively slender to moderately thick. The umbilicus is wide and shallow with a low and rather shallowly inclined umbilical wall. The whorls are low. Their height, and also width, increases only slowly in the course of ontogeny. Sculpture is coarse and with broad interrib spaces (there are about 11 high bullae per whorl in the adult growth stage). Adult external suture line similar to that of *P. keyserlingi*.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
Holotype	105	35(33)	31(29)	39(37)	41	—
BGR, kv 347	99	34(34)	26(26)	39(39)	35	40
BGR, kv 345	106	40(38)	29(27)	37(35)	41	45?
BGR, kv 346	121	43(36)	33(27)	44(36)	—	44

Discussion. The holotype of this remarkable and easily recognizable species was very well refigured by Koenen (1902, Pl. 50, figs. 4, 5). Further indications about its morphology are provided by the illustrations of numerous synonymous taxa erected by Koenen (1909; see in the synonymy).

The specimens in the BGR collections in Hannover are only tolerably well preserved. They exhibit definite phenomena of senility, which attest their adult nature. The adult size of the species measures, therefore, about 120 mm. The living chamber comprises almost the entire length of one whorl. The whorls are low and always wider than high. As the width of the whorl only increases very slowly the shell is relatively thin. The specimen BGR, kv 345 is undeformed at the beginning of the last whorl. Its flanks and venter are regularly arched at this point. The convexity of flanks may apparently lessen somewhat in other specimens. However, it is not certain whether this impression of less convex flanks is not caused by their deformation.

The umbilical shoulder is always broadly rounded and the convex umbilical wall is more or less gently inclined. The inclination increases in the course of ontogeny to reach a maximum on the adult living chamber. The umbilicus is accordingly broad and shallow. Because of the broad rounding of the umbilical shoulder, the umbilicus has a funnel-like rather than a step-like appearance.

The sculpture of early growth stages is unknown. Bullae appear already very early and are strongly developed. Their number is small and comprises less than 15 per whorl. They are particularly high and strongly developed on the living chamber where they number about 12 per whorl. The ribbing becomes indistinct on the living chamber where the number of ribs is reduced. At the beginning of the living chamber occur rib bundles with an increased number of ribs (i.e. with four to six supplementaries). The rib bundle of this area consists of a bifurcating rib with a simple rib either in front or behind and a trivirgatitpartitous element (e.g. BGR, kv 347).

Only terminal, adult external suture lines of *Polyptychites brancoi* (Neumayr and Uhlig 1881) were available for study in the BGR collections. These were studied in the specimens kv 345, 346 and 347 where they immediately precede the adult living chamber at shell diameters ranging from 95 to 105 mm.

The denticulation of their lobes and saddles are similar to that of the morphologically conservative representatives of *P. keyserlingi* and to that of *P. pavlowi* as the relatively short and sturdy lobules of the lateral saddles and the lateral and terminal branches of the lateral lobes are either distinctly notched or secondarily denticulated. The auxiliary lobes and saddles are either simply and very shallowly denticulated or merely notched. However, two out of three sutures studied have three auxiliary lobes. This suggests that the adult external sutures of *P. brancoi* are more advanced than those of the conservative representatives of *P. keyserlingi* and those of *P. pavlowi*.

The shape and proportions of lobes and saddles vary extremely strongly. One extreme is represented by the specimen BGR, kv 347 (Figure 21b). There the lateral lobes are from 3 to 3 1/2 times longer than wide and have very long and slender terminal branches. These lateral lobes approach closely the still more attenuated lateral lobes of the holotype of *P. brancoi* (Neumayr and Uhlig, 1881, p. 156; Pl. XXVI, fig. 1). The lateral saddles of this extreme variant are square-shaped and widened considerably in comparison with those of all other sutural variants of *P. brancoi*. In specimen BGR, kv 347 the first lateral saddle is about as wide as the broad and sturdy ventral lobe and about 1 1/2 times wider than the attenuated first lateral lobe. The second lateral saddle is about 1 1/2 times wider than the first lateral lobe.

The first and second auxiliary lobes of this specimen, of which the first is situated directly on the umbilical shoulder while the second occurs in the middle of the umbilical wall, are slender, parallel-flanked structures. The first auxiliary is half as large as the second lateral lobe. Its shape and denticulation are similar to those of the latter. The second auxiliary is a slender (three times longer than it is wide), almost regularly trifid structure that is only shallowly notched on the flanks. It is about half as large as the first auxiliary. The third auxiliary lobe, which is situated in the proximity of the umbilical seam, is an irregularly shaped, apparently bifid, roundtipped structure that is twice as wide as it is high (Figure 21b). This odd shape may be caused by a malformation.

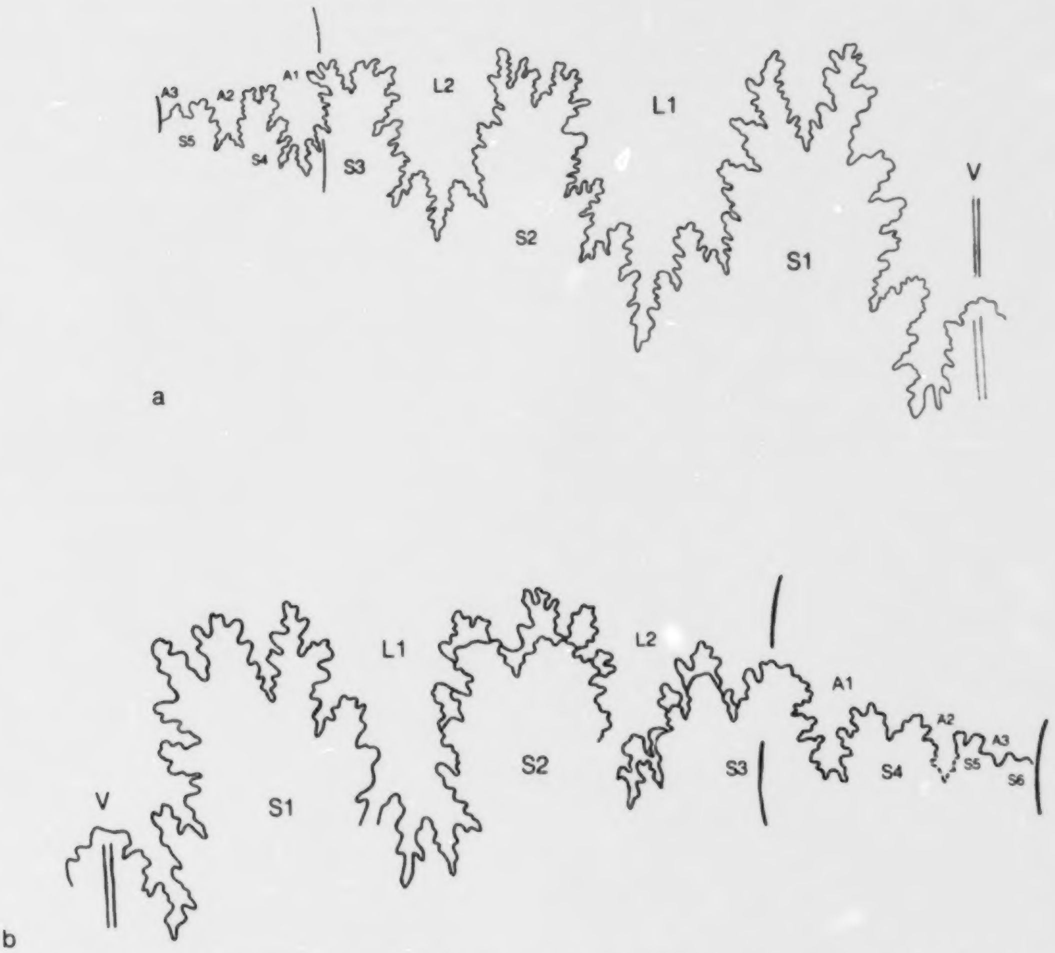


Figure 21. Adult external suture lines of *Polyptychites brancoi* (Neumayr and Uhlig, 1881). **a**. Specimen BGR kv 346 from Bueckeburg-Jetenburg, Northwest Germany. Lower *Polyptychites*-Beds, mid-early Valanginian. The terminal suture behind the adult living chamber at the whorl height (wh) of about 32 mm, x 2 (approx.). **b**. Specimen BGR kv 347. The same locality and age as for BGR kv 346. The terminal suture behind the adult living chamber at the whorl height (wh) of about 29 mm, x 3 (approx.).

The third and fourth lateral saddles are at least two and a half times wider than the preceding lobes. Their essentially flat tops each bear only one subcentrally situated, fairly large and markedly notched lobule. Furthermore, they bear a few simple and shallow notches each. The fifth lateral saddle is, in contrast, only slightly wider than the preceding second auxiliary lobe. However, this may be related to the strongly widened, possibly malformed shape of the third auxiliary. The exposed part of the sixth lateral saddle is about as wide as the third auxiliary lobe. Its top is sinuous but does not exhibit any clearly defined notches. No part of the fourth auxiliary lobe was observed at the umbonal seam.

The other morphological extreme is represented by the specimen BGR, kv 346 (Figure 21a), the lateral lobes of which are short and sturdy (only about 1 1/2 times longer than wide), pronouncedly tapering apicalward (i.e. broadly conical) structures. No similarly shaped and proportioned lateral lobes are known in any of the representatives of *P. brancoi* figured by Koenen (1909; see the synonymy for further details). However, these lobes match closely the still sturdier and less denticulated lateral lobes of *P. keyserlingi* var. *scalarinus* figured by Koenen (1909, Pl. X, figs. l, 2). The ventral lobe of the specimen BGR, kv 346 also tapers adapically and is distinctly shortened in comparison with that of kv 347 (Figure 21b). All lobes, beginning with the ventral lobe, decrease in size approximately evenly all the way to the umbilical seam.

The first auxiliary of kv 346 is situated on the inner side of the umbilical shoulder and the outermost umbilical wall while the second auxiliary is situated in the middle of the umbilical wall. These two auxiliaries are also sturdy and short (about twice as long as they are wide), shallowly denticulated structures. They taper less adapically than do the lateral lobes and their tips are irregularly trifid. Only the outer flank of the third auxiliary lobe is exposed at the umbilical seam. This apparently round-tipped, only slightly notched structure tapers pronouncedly adapically.

The first to fourth lateral saddles of BGR, kv 346 are wedge-shaped and widen markedly to distinctly adapically. All of them are relatively narrowed in comparison with their equivalents in BGR, kv 347 and are considerably more narrow (up to two times) than the preceding lobes. Their narrow tops bear a solitary major lobule each that is simply and shallowly denticulated. The fifth lateral saddle, which occupies the inner half of the umbilical wall, is appreciably widened relative to the preceding saddles and has a flat top. It also bears a solitary centrally situated lobule that is only slightly notched.

The unfigured adult suture line of specimen BGR, kv 345 appears to be morphologically transitional between those of the specimens BGR, kv 347 and kv 346. Its lateral and auxiliary lobes are almost as short and sturdy as those of specimen BGR, kv 346 (i.e. only about 1 1/2 times longer than wide). However, they are all parallel-sided and appreciably more deeply and more complexly denticulated than the equivalent lobes of BGR, kv 346. The two auxiliary lobes of the specimen BGR, kv 345 are positioned like their equivalents in the other two specimens. They are even more similar to their equivalents in BGR, kv 347 than are the lateral lobes. No part of the third auxiliary lobe was observed at the umbilical seam.

The ventral and lateral parts of the terminal suture line of *P. brancoi* var. *schmidti* figured by Koenen (1909, Pl. XI, figs. 3, 4) apparently differ from those of BGR, kv 345 only in a somewhat greater width and more marked adapical tapering of the first lateral lobe. The suture appears to be transitional between the sutures of BGR, kv 345 and kv 346. The saddles are either only slightly more narrow than those of kv 347 or of similar width. However, their denticulation is about as shallow, simple and sparse as that of kv 345.

The orientation of the suture lines varies markedly. The suture of BGR, kv 345 is straight and pronouncedly ascendant (at about 30 degrees) throughout the flank (including the first auxiliary lobe). Its umbilical part is subradial and the two portions meet at an angle.

The suture lines of BGR, kv 346 and 347 are, in contrast, only distinctly ascendant (at 10 to 15 degrees) in their lateral parts ending with the second lateral lobes and then become equally distinctly descendant. The junction of these segments has a shallowly arched appearance.

Most of the adult sutures are moderately widely (BGR, kv 345) to narrowly (BGR, kv 346) separated. However, those of BGR, kv 347 (Figure 21b) either touch or overlap through most of their extent.

In spite of the scarcity of the material, it appears evident that the adult external suture lines of *Polyptychites brancoi* are just as variable as those of the closely related *P. keyserlingi*. Furthermore, the extreme variants are similar in the two species. Contrary to the opinion of Neumayr and Uhlig (1881, p. 156), the strong attenuation of lateral lobes is not diagnostic of the species as a whole.

Affinities and differences. *P. brancoi* undoubtedly evolved from *P. pavlowi*: its differentiation from that species has been discussed already. *P. brancoi* cannot be confused with any other *Polyptychites* species.

The species is recorded from Northwest Germany, Eastern England (Speeton) and the Pechora Region.

Polyptychites lamplughi Pavlow 1892

Pl. 7, fig. 1; Figures 22, 23.

*1892	*Olcostephanus (Polyptychites) lamplughi* Pavlow in Pavlow and Lamplugh, p. 485-487, Pl. 14, figs. 1a-1c (non Pl. 15, figs. 1a, 1b).
?1902	*Olcostephanus keyserlingi* Bogoslovsky, p. 118, 119, Pl. 1, figs. 1a-1c.
non 1909	*Polyptychites lamplughi* Koenen, p. 46-48, Pl. 19, figs. 1, 2.

Lectotype. The specimen figured by Pavlow in Pavlow and Lamplugh 1892, Pl. 14, figs. 1a-1c is herewith designated formally as the lectotype of *Polyptychites lamplughi*. This designation has already been made informally by Koenen (1909) and Spath (1924). Koenen (1909, p. 46) expressly excluded Pavlow's other specimen (in Pavlow and Lamplugh, 1892, Pl. 15, fig. 1) from the species. Spath (1924, p. 75) then assigned the excluded speccimen to a new species, *P. pyritosus*. This action left only the specimen figured in Pl. 14, fig. 1a-1c in *P. lamplughi*. The lectotype, formerly in Scarborough Museum, is believed to be lost.

Locus typicus. Speeton, Eastern England.

Stratum typicum. Unknown.

Material. 8 specimens from the *Polyptychites*-Beds (lower Valanginian) of Bueckeburg-Jetenburg and Lindhorst are in the BGR collections, Hannover.

Diagnosis. A medium-sized species of *Polyptychites* with a relatively wide (about 33 per cent) umbilicus and moderately wide whorls. The increase of the width of whorls diminishes in advanced growth stages. The umbilical wall is never steeply inclined; it is, on the contrary, gently inclined and convex as compared with other representatives of the genus. The umbilicus is, therefore, funnel — rather than step-shaped. The adult external suture line is *P. oerlinghusanus*-like.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
BGR, kv 84	90	30(33)	25(23)	35(39)	37	46
BGR, kv 83	119	38(32)	38(32)	43(36)	51	63
BGR, kv 85	117	39(33)	34(29)	43(37)	55	61

Description. The species was described comprehensively by Pavlow (in Pavlow and Lamplugh, 1892, p. 485, 486). The German material agrees very well with Pavlow's (l. cit.) drawing, except that most specimens (e.g. BGR, kv 269) are not as broad-whorled as the lectotype in the adult growth stage. The lectotype is, therefore, a variant which becomes relatively wide-whorled when adult. There is a comparable broad-whorled variant from Northwest Germany in BGR collections, Hannover (kv 270).

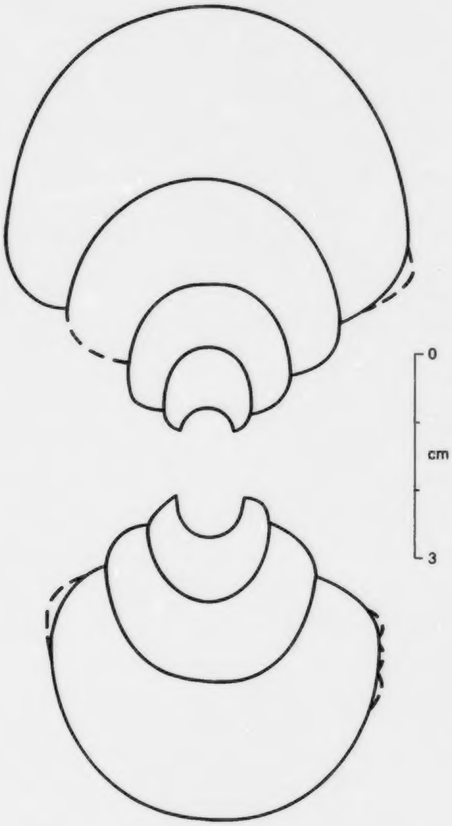


Figure 22. Cross-section of *Polyptychites lamplughi* (Pavlow, 1892). Specimen BGR kv 325, Lindhorst clay pit, Northwest Germany. *Polyptychites*-Beds, early Valanginian. Note the linear scale.

The living chamber reaches a length of one whorl. The whorl is always wider than high. However, contrary to *P. keyserlingi*, *P. lamplughi* exhibits a tendency to a relative decrease of the whorl's width in adulthood (Figure 22). The whorls are broadly rounded adventrally, forming a "Roman arch". The greatest width of the whorl is situated at the level of the pronouncedly rounded umbilical shoulder. As compared with other species of *Polyptychites*, the umbilical wall is rather gently inclined. It is more or less pronouncedly convex, especially during young and intermediate growth stages. Therefore, and because the succeeding whorls strongly enclose the preceding ones, the umbilicus is funnel- rather than step-shaped. It has, at the same time, a relatively shallow appearance.

The adult external suture line, as exemplified by specimen BGR, kv 84 (Pl. 7, fig. 1; Figure 23) and the holotype (Pavlow in Pavlow and Lamplugh, 1892, Pl. XIV, fig. 1c), is of the same conservative polyptychitinid type as that of *P. pavlowi* where the shape and proportions of all its elements are concerned. However, all elements of this suture line are appreciably to much (i.e. in specimen BGR, kv 84; see below for further details) less complexly and deeply denticulated than those of the *P. pavlowi* suture. They are only similar in these respects to the corresponding elements of the otherwise more advanced suture line of *P. oerlinghusanus*. The adult external sutures of *P. pavlowi* and *P. lamplughi* must be classified as the morphologically simplest (?most primitive) sutures known in the genus *Polyptychites* in these respects. However, like the adult external suture line of *P. oerlinghusanus*, that of *P. lamplughi* is more advanced in that it already possesses three auxiliary lobes.

The suture line of the German specimen BGR, kv 84 (Pl. 7, fig. 1A; Figure 23) is even more shallowly and less complexly denticulated than that of the holotype (Pavlow

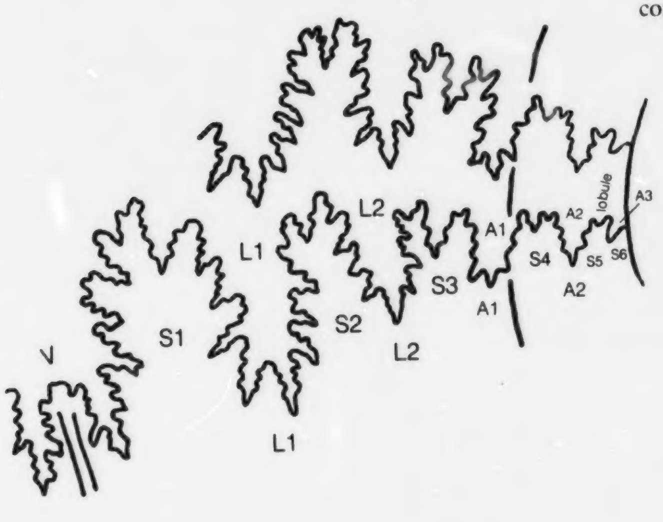


Figure 23. Adult external suture line of *P. lamplughi*. Specimen BGR kv 84 reproduced in Pl. 7, fig. 1 (see its description for further details). Two early adult sutures exposed on the intermediate whorl at the height (wh) of about 27 mm, x 2 (approx.).

in Pavlow and Lamplugh, 1892, Pl. XIV, fig. 1c). All its lobules, excluding the terminal prongs of the ventral lobe, are short triangular-shaped structures complicated by barely discernible notches. The lobules of the holotype are considerably longer and more slender. Furthermore, they bear small but clearly discernible second order lobules instead of slight notches. These distinctions do not appear to be caused by the state of preservation of the specimens concerned and are ascribed tentatively to infraspecific variation.

The first lateral lobe of BGR, kv 84 is only slightly shorter and narrower than the ventral lobe. It is short and sturdy (its length is 2 to 2 1/2 times greater than the width), tapers distinctly apicalward and is almost symmetrically trifid. The second lateral lobe is entirely similar to the first but only about half as large. The first auxiliary lobe is again similar but its size is about two-thirds that of the second lateral lobe. This auxiliary lobe is situated either on the lowermost (i.e. adumbilicalmost) part of the flank or on the umbilical shoulder. The second auxiliary lobe is a short and sturdy (about as long as it is wide), triangular-shaped structure, the size of which is somewhat less than one-half that of the first auxiliary lobe. The second auxiliary lobe occupies the middle of the umbilical wall and is separated from the umbilical seam by an about equally wide fifth lateral saddle. The middle part of the top of this saddle is occupied by a lobule, which is a small and simple, triangular-shaped structure that is about as wide as it is high. The third and last auxiliary lobe is situated at the umbilical seam with only the outermost part of the sixth lateral saddle showing behind it. This lobe is about twice as long as it is wide, simple and triangular-shaped. Its length and width comprise about one-third those of the second auxiliary.

The auxiliary part of the suture line is also clearly visible on the exposed part of the preceding whorl of BGR, kv 84 where it has the above described appearance.

The first to fourth lateral saddles distinctly expand apicalward in accordance with the tapering of the flanking lobes. They are all subdivided in two by solitary lobules which are short and subcentrally located. The first and second lateral saddles are either as wide as or but slightly wider than the preceding lobes while the third and fourth lateral saddles are from one and a half to two times wider than the preceding lobes.

The lateral part of the suture line ending with the second lateral lobe is slightly (5 to 10 degrees) ascendant while its auxiliary part is either subradially oriented or slightly descendant. The orientation changes gradually which results in a forward-convex appearance of the imaginary line connecting the tops of saddles.

The adult external suture line of the British holotype (Pavlow, in Pavlow and Lamplugh, 1892, Pl. XIV, fig. 1c) only differs from that of BGR, kv 84 in much sturdier proportions and the downward tapering shape of its first lateral lobe. The presence of the third auxiliary lobe is not indicated in the drawing. However, there is ample room for it between the lobule of the fifth saddle and the indicated position of the umbilical seam.

Strong development of bullae is a prominent feature of the sculpture. The bullae develop from the primary ribs early in ontogeny (at a shell diameter of about 30 mm). In specimen BGR, kv 84 (Pl. 7, fig. 1) the penultimate whorl has 18 and the ultimate whorl 17 bullae while BGR, kv 83 has 17 and 16 and BGR, kv 85 has 18 and 17 bullae respectively. The bullae extend far onto the umbilical wall; mostly right to the umbilical seam. These extensions of bullae are approximately radially oriented on the early whorls. On the more advanced growth stages they are more or less pronouncedly bent forward. The bullae are considerably sharpened on the intermediate growth stages and are distinctly elevated just before the umbilical shoulder. The strongly expressed, acutely pointed appearance of the bullae is lost (except for BGR, kv 84) on the penultimate and ultimate whorls, where they become swollen.

It was not possible to observe the ornamentation of early and intermediate growth stages in the material available. There are four secondary ribs in most bundles of advanced whorls. The bundling habit has an irregularly bidichotomous appearance when the subdivision points are situated more addorsally (e.g. BGR, kv 84; Pl. 7, fig. 1). However, in BGR, kv 83 and kv 85 the subdivision points are situated so close to the bullae that their bundles have a fasciculate rather than a bidichotomous appearance. The number of secondaries may increase to five in some bundles. In the adult growth stage the number of secondary ribs is again reduced to 3. The arrangement of secondaries in this stage — as always in the adult — is very irregular.

Affinities and differences. *P. lamplughi* differs from its ancestral species *P. pavlowi* first of all in its considerably broader whorls. Furthermore, its adult external suture line has three auxiliary lobes. From *P. brancoi* it differs also in relatively broader whorls as well as in a more dense sculpture and a greater number of bullae per whorl. An essential difference from *P. keyserlingi* consists in the rate of widening of the whorl in advanced growth stages. Finally, it differs from *P. clarkei* in considerably wider whorls with a broadly arched cross-section. *P. lamplughi* cannot be confused with any other *Polyptychites* species.

Polyptychites keyserlingi (Neumayr and Uhlig 1881)

Pl. 5, fig. 4; Pl. 6, figs. 1-4; Pl. 26, figs. 2, 5; Figures 24, 25.

*1881	*Olcostephanus Keyserlingi* Neumayr and Uhlig, p. 155, 156, Pl. 27, figs. 1-3.
1892	*Olcostephanus (Polyptychites) Keyserlingi* Pavlow, in Pavlow and Lamplugh, p. 478-479 (pars), Pl. 8, figs. 13a, b; Pl. 16, figs. 1a-1c.
1892	*Olcostephanus (Polyptychites) Lamplughi* Pavlow, in Pavlow and Lamplugh, p. 485-488 (pars), Pl. 15, figs. 1a, b (non Pl. 14, figs. 1a-1c).
non 1892	*Olcostephanus (Polyptychites) Keyserlingi* Pavlow, in Pavlow and Lamplugh, p. 478, 479 (pars), Pl. 15, figs. 5a-5c.

non 1902	*Olcostephanus Keyserlingi* Bogoslovsky, p. 118, 119, Pl. 1, figs. 1a-1c.
?1902	*Olcostephanus* cf. *polyptychus* Bogoslovsky, p. 132, 133, Pl. 13, fig. 3.
non 1902	*Olcostephanus* cf. *Keyserlingi* Bogoslovsky, p. 133, Pl. 14, figs. la, b.
?1902	*Olcostephanus* aff. *Keyserlingi* Bogoslovsky, p. 133, Pl. 14, figs. 2a, b.
?1902	*Olcostephanus Michalskii* varietas *tuberculata* Bogoslovsky, p. 135, Pl. 15, figs. 4a, b.
?1902	*Olcostephanus* cf. *Michalskii* var. Bogoslovsky, p. 135, Pl. 15, figs. 6a-6c.
non 1902	*Olcostephanus* aff. *Keyserlingi* Bogoslovsky, p. 133, Pl. 18, figs. 4a, b.
1902	*Polyptychites laticosta* Koenen, p. 141, 142, Pl. 1, figs. 5-7.
non 1902	*Polyptychites Keyserlingi* Koenen, p. 131-134, Pl. 2, figs. 2-4.
1902	*Polyptychites bullatus* Koenen, p. 138-140, Pl. 48, figs. 1a, b.
1902	*Polyptychites Keyserlingi* Koenen, p. 131-134, (pars), Pl. 49, figs. 1, 2 (re-figuring of the lectotype).
1902	*Polyptychites latissimus* juv. Koenen, p. 129-131 (pars), Pl. 54, figs. 1a, b.
non 1906	*Olcostephanus (Polyptychites)* cf. *Keyserlingi* Danford, Pl. 10, figs. 3, 3a.
1909	*Polyptychites infundibulum* Koenen, p. 16, 17, Pl. 3, figs. 1, 2.
1909	*Polyptychites robustus* Koenen, p. 43-45, Pl. 3, figs. 3, 4.
1909	*Polyptychites costellatus* Koenen, p. 23-25, Pl. 9, figs. 1, 2.
1909	*Polyptychites scalarinus* Koenen, p. 26-28, Pl. 10, figs. 1, 2.
1909	*Polyptychites inflatus* Koenen, p. 18-19, Pl. 10, figs. 3, 4.
1909	*Polyptychites arcuatus* Koenen, p. 28, 29, Pl. 11, figs. 2, 4.
1909	*Polyptychites acuticosta* Koenen, p. 30, 31, Pl. 12, figs. 1, 4.
1909	*Polyptychites suessi* Koenen, p. 76, 77, Pl. 12, figs. 2, 3.
1909	*Polyptychites coronula* Koenen, p. 57, 58; Pl. 13, figs. 2, 3.
1909	*Polyptychites sinzowi* Koenen, p. 35, 36; Pl. 14, figs. 1, 4.
1909	*Polyptychites tschernyscheffi* Koenen, p. 62-64; Pl. 14, figs. 2, 3.
1909	*Polyptychites salchowi* Koenen, p. 37-38, Pl. 15, figs. 1, 4.
1909	*Polyptychites spinulosus* Koenen, p. 38, 39, Pl. 16, figs. 3, 4.
1909	*Polyptychites marginatus* Koenen, p. 25, 26, Pl. 17, figs. 3, 4.
1909	*Polyptychites senilis* Koenen, p. 50, 51, Pl. 20, figs. 1, 5.
?1909	*Polyptychites keyserlingi* Koenen, p. 51, 52, Pl. 21, figs. 1, 2.
1909	*Polyptychites solidus* Koenen, p. 52, 53, Pl. 22, figs. 1, 2.
1924	*Polyptychites pyritosus* Spath, p. 75 (pro *P. lamplughi* Pavlow, 1892, Pl. 15, figs. 1a, b non Pl. 14, figs. 1a, b).
1924	*Polyptychites subgravesi* Spath, p. 75 (pro: *P. keyserlingi* Pavlow, 1892, Pl. 16, figs. 1a-1c).
non 1931	*Polyptychites Keyserlingi* Sokolov and Bodylevsky, p. 96, Pl. 11, figs. 1a, b.
non 1931	*Polyptychites* aff. *Keyserlingi* Sokolov and Bodylevsky, p. 96, 97, Pl. 12, figs. 1a, b.
1931	*Polyptychites* cf. *infundibulum* Sokolov and Bodylevsky, p. 97, 98, Pl. 13, figs. 1a, b.
1960	*Polyptychites* aff. *polyptychus* Klimova, p. 173, 174 (pars), Pl. 21, fig. 6.
1964	*Polyptychites keyserlingi* var. *pavlowi* Jeletzky, p. 40, Pl. 6, figs. 3A, B.
1964	*Polyptychites keyserlingi* f. typ. Jeletzky, p. 40, Pl. 6, figs. 6A, B.
?1964	*Polyptychites* cf. *keyserlingi* Jeletzky, p. 40, Pl. 6, figs. 2A, 2B; 5.
1965b	*Polyptychites keyserlingi* var. *pavlowi* Jeletzky, p. 6, Pl. 1, figs. 2A, B.
1965b	*Polyptychites keyserlingi* s. lato Jeletzky, p. 6, Pl. 1, fig. 3.
1965b	*Polyptychites keyserlingi* f. typ. Jeletzky, p. 6, Pl. 1, figs. 4A, B.
1967	*Polyptychites* aff. *michalskii* Bodylevsky, p. 111, Pl. 9, figs. 4a, b.
1968	*Polyptychites keyserlingi* Kemper, p. 31, Pl. 22, fig. 4.
1968	*Polyptychites michalskii* Kemper, p. 31, Pl. 25, figs. 5a, b.
1973	*Polyptychites (Polyptychites) keyserlingi* Jeletzky, p. 67-70, Pl. 1, fig. 2; Pl. 3, figs. 2a, b.
1975	*Polyptychites keyserlingi* Kemper, p. 248, 249.
1976	*Polyptychites keyserlingi* Kemper, p. 34, Pl. 22, fig. 4.
1976	*Polyptychites* juv. sp. indet. Kemper, p. 34, Pl. 25, figs. 5a, b.
1977	*Polyptychites keyserlingi* Kemper, p. 3, 4, fig. 2.
?1977	*Polyptychites* cf. *lejanus* Thieuloy, p. 412, Pl. 6, fig. 11.
1978	*Polyptychites (Polyptychites) keyserlingi* Surlyk, p. 33, Pl. 8, fig. 2.

Lectotype. Selected herein the original of Neumayr and Uhlig, 1881, Pl. 27, fig. 1, 1a, which was well re-figured by Koenen (1902, Pl. 49, figs. 1, 2). The specimen is preserved in the Roemer-Museum, Hildesheim, Federal Repulbic of Germany. A cast is preserved in BGR collection as No. kv 266.

Locus typicus. Flegessen at Suentel.

Stratum typicum. Lower Valanginian.

Material. Some 200 specimens in the collection of the Geological Survey of Lower Saxony. Many times that number is present in toto in various museums of Germany alone. Of these collections that of the Geological Institute, Goettingen is the most important. The most important localities in Northwest Germany were Bueckeburg-Jetenburg and Lindhorst.

Diagnosis. A medium-sized, morphologically highly variable species of *Polyptychites*. It has a tendency to develop broad and very coarsely sculptured adult whorls, which rapidly increase in width in the course of ontogeny. However, only its evolutionarily progressive variants are characterized by this development. The sculpture is, generally speaking, relatively coarse. Primary ribs are transformed into typical bullae early in ontogeny. Rib bundles of penultimate whorl only rarely consist of more than 4 secondary ribs per bundle.

Measurements (in mm).

Specimen	Whorl diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
Holotype (prog.)	103	32(31)	30(29)	41(40)	43	62
BGR, kv 81 (prog.)	89	26(29)	28(31)	36(40)	42	50
BGR, kv 82 (prog.)	95	28(29)	32(34)	36(38)	—	—
BGR, kv 75	72	22(30)	23(32)	29(40)	30	37
BGR, kv 80	73	25(34)	21(29)	26(36)	33	38
BGR, kv 79	61	19(31)	18(30)	24(39)	26	34
BGR, kv 69	77	23(30)	24(31)	29(38)	—	36

Description. Together with *P. pavlowi* this medium-sized species includes the bulk of *Polyptychites* in Northwest Germany. Should *Polyptychites* have been erected in this region it is certainly this species, and not *P. polyptychus*, that would have been designated as its type species. Because of the doubtful nature of *P. polyptychus*, one must recommend a study of figures of *P. keyserlingi* in order to recognize the typical features of the genus *Polyptychites*. The species exhibits a considerable variability in shell shape and ornament (Pl. 6, fig. 1-4; Figure 24). The holotype is one of the extremely broad variants, which are characterized by a particularly coarse sculpture in adult whorls (see Pl. 5, fig. 4). The same holds true for the bulk of Koenen's (1902, 1909) new "species", which are returned herein into the synonymy of *P. keyserlingi*. A study of these numerous figures (it is only rarely that so many illustrations are available for a single species) provides an idea of the variability of this species in the adult state.

As already mentioned in the discussion of the genus *Euryptychites*, the advanced stages of ontogenetic development may result in the appearance of *Euryptychites*-like shell proportions. The irregularity and coarseness of the adult sculpture provides a distinguishing character in such instances as the adult sculpture remains more refined and more regular in all presently known representatives of *Euryptychites*. An example of such an extremely thick *P. keyserlingi* form is provided by the specimen figured by Koenen (1909, Pl. 17, figs. 3, 4) as *P. "marginatus"*. Another specimen, figured by Koenen (1909, Pl. 12, figs. 1, 4) as *P. acuticosta*, exhibits the wide-whorled adult stage of a widely umbilicate extreme variant. The specimen figured by Koenen (1909, Pl. 12, figs. 2, 3) as *P. suessi* is an adult of a narrowly umbilicate extreme variant of our species.

The forms with broad (or wide) adult whorls are considered herein as morphologically progressive variants of the species (Pl. 5, fig. 4). The tendency to an increase in the width of the whorls in advanced growth stages is an important feature of the species. In spite of the overwhelming number of illustrations available in the literature, the impression obtained of the species in this way is incomplete, because it is predominantly the largest and most progressive specimens that were singled out and figured. The bulk of the material available in German collections is smaller and less striking. This relatively less progressive material, which only partly consists of non-adult specimens, will be subject of special attention in this paper. Representatives of this material are figured herein (Pl. 6, figs. 1-4).

So far as the progressive variants of *P. keyserlingi* are concerned (e.g. Pl. 5, fig. 4), the reader is referred to the numerous descriptions and figures of Koenen (1902, 1909) listed in the synonymy and Figure 24.

The bulk of the material is characterized by shell diameters of about 100 mm and an umbilical width of around 31 per cent of the diameter. The whorls are substantially wider than they are high and are regularly arched (forming a "Roman arch") in the adventral region. The umbilical shoulder is broadly rounded. The umbilical wall is distinctly convex and very steeply oriented. In the adult growth stage it becomes oriented at an acute angle to the shell's diameter and considerably higher (Figure 24, BGR, kv 321).

The tendency to an increase in whorl width in the adult state is seen in most specimens. It is, however, considerably more weakly expressed in most than in the extreme variants. The maximum width of the whorl is situated at the level of the umbilical shoulder. The umbilicus is always step shaped and, depending on the degree of increase of the whorl's width, moderately to rather deep. The enclosure of preceding by succeeding whorls varies between 65 and 77 per cent. The living chamber always exceeds the length of one whorl.

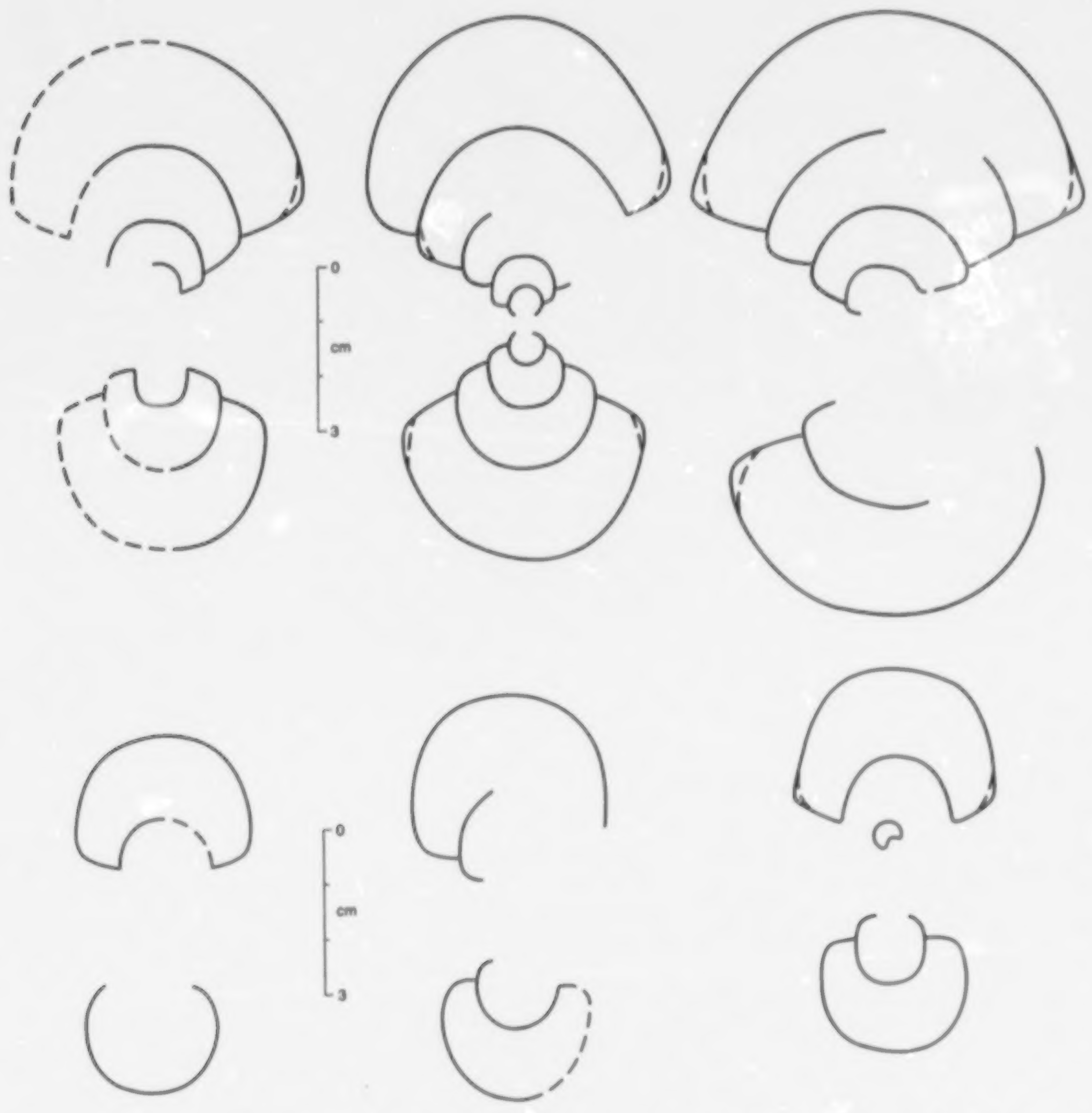


Figure 24. Variability of the adult cross-section of *Polyptychites keyserlingi* (Neumayr and Uhlig, 1881). Progressive variants are represented by the specimens (from left to right) BGR kv 375 (Lindhorst clay pit), BGR kv 320 (Lindhorst clay pit) and BGR kv 321 (Bueckeburg-Jetenburg clay pit) in the upper row. The conservative variants are represented by the specimens (left to right) BGR kv 316 (Jetenburg-Bueckeburg clay pit), BGR kv 317 (Lindhorst clay pit), and BGR kv 374 (Jetenburg-Bueckeburg clay pit) in the lower row. Note the linear scale. All from *Polyptychites*-beds, upper lower Valanginian.

The following evaluation of adult external suture lines of *Polyptychites keyserlingi* is based in part on the numerous photographs published by Koenen (1909) of ammonites placed in *P. keyserlingi* by the writers (see synonymy). Less numerous (about 10 in all) specimens of *P. keyserlingi* preserved in BGR collections and exhibiting reasonably well preserved adult (mostly only the last few sutures) external suture lines are even more valuable. These ammonites have also provided some stratigraphical information critical for the evaluation of evolutionary development of the suture line.

With one exception (Neumayr and Uhlig, 1881, Pl. XXVII, fig. 2a), no earlier adult suture lines were available for study.

This detailed study of the adult suture line of *P. keyserlingi* is most important for the taxonomic and stratigraphic evaluation of its Canadian representatives described in the second part of this paper, as their sutures (Figure 47a) belong to a morphologically extreme, presumably phylogenetically advanced type.

Like all other morphological features of *P. keyserlingi*, its adult external suture line is extremely variable. The following account outlines both morphological extremes and intermediate variants.

Koenen's (1909) photographs are a somewhat defective source of information. All the suture lines were outlined by paint on the specimens concerned and then photographed with them. This has caused a considerable distortion of their elements because of the globose nature of the specimens. Furthermore, only the lateral elements and the first auxiliary lobe of these suture lines were marked as a rule. The character of the remaining elements had to be inferred from indirect evidence (see below).

The external suture lines of the BGR specimens are commonly incomplete in their auxiliary parts and are frequently strongly distorted throughout, because of a partial caving in of the phragmocone. The writers believe, however, that Koenen's (1909) photographs and the sutures studied here do provide a fair idea of the range of variation of the adult external suture line.

One morphological extreme is exemplified by the suture line of *P. keyserlingi* var. *robustus* Koenen (1909, Pl. II, fig. 3) and specimen BGR, kv 338 (Figure 25b) This suture resembles rather closely the adult sutures of *P. pavlowi* and *P. lamplughi* and belongs to the same morphologically (and presumably evolutionarily) conservative type of *Polyptychites* suture line. Its relatively wide and short lobes tend to taper markedly adapically. The intervening saddles expand correspondingly adapically. The depth and degree of complexity of denticulation of all elements of this suture is about the same as in *P. pavlowi* and *P. lamplughi*. Furthermore, the same is true of the orientation of this suture line and the shape and proportions of its lobes and saddles.

The first and second lateral saddles are either as wide as the preceding lobes or only slightly wider than they. Only the first and second lateral lobes are situated on the shell's flank. The third lateral saddle is, in contrast, at least two times wider than the second lateral lobe (Figure 25b). It mostly occupies the lower quarter of the flank and at least all of the umbilcal shoulder but may extend (e.g. Koenen, 1909, Pl. II, fig. 3) onto the outermost part of the umbilical wall. The first auxiliary lobe may, therefore, be situated anywhere between the outermost and the middle part of the umbilical wall. This lobe is followed by the fourth lateral saddle, which is at least twice as wide as the preceding lobe (e.g. BGR specimen kv 338; Figure 25b), and then by the second auxiliary lobe. The latter is situated almost at the umbilical seam, from which it is only separated by the outer part of the fifth lateral saddle subdivided by one or two fairly large to tiny lobules. The largest examples of these lobules may give the impression of an incipient third auxiliary lobe.

The external suture line of the medium-sized cotype of *P. keyserlingi* figured by Neumayr and Uhlig (1881, Pl. XXVII, fig. 2a) and that of its large specimen figured by Koenen (1902, Pl. II, figs. 2, 4) and reproduced in Figure 25d are similar to the suture of the above described BGR specimen. However, they are even more typical of that variant in the absence of an oversized lobule in the fifth lateral saddle. Because of a narrow interval that separates the first auxiliary lobe from the umbilical seam in *P. keyserlingi* var. *robustus* and other similar figured specimens (e. g. *P. k.* var. *senilis*; Koenen, 1909, Pl. XX, fig. 4), the nonvisible auxiliary parts of their suture lines are also assumed to include only the second auxiliary lobe.

Another morphological extreme, designated here the morphologically and evolutionarily progressive variant, is represented by the suture lines of *P. k. arcuatus* Koenen (1909, Pl. XI, fig. 1), *P. k.* var. *suessi* Koenen (1909, Pl. XII, fig. 3), *P. k.* var. *spinulosus* Koenen (1909, Pl. XVI, fig. 1), *P. k.* var. *solidus* Koenen (1909, Pl. XXIII, fig. 2), BGR, kv 337 (Figure 25c), and BGR, kv 339 (Figure 25a). These sutures have appreciably to much more slender and long, subparallel-flanked lobes and approximately square-shaped saddles. The two lateral lobes and the first auxiliary lobe are mostly situated on the shell's flank. The first auxiliary occurs mostly, anywhere between the top of the bulla (e.g. in *P. k. spinulosus* and *P. k. suessi*) and its base (e.g. in *P. k. arcuatus* and BGR, kv 339). In such typical instances illustrated by the Figure 25a, the fourth lateral saddle extends over the umbilical shoulder and the outer part of the umbilical wall whilst the second auxiliary is situated either within the middle or within the outer part of the umbilical wall. Only in BGR, kv 337 (Figure 25c) and *P. k. solidus* (Koenen, 1909, Pl. 23, fig. 2), where the first auxiliary lobe straddles the umbilical shoulder, is the relatively narrowed fourth lateral saddle restricted to the outer part of the umbilical wall.

The umbilical part of this extreme variant of the suture is exemplified by the specimens BGR, kv 337 and kv 339. In these completely exposed sutures the fourth lateral saddle is followed by shallowly denticulated and distinctly adventrally inclined second auxiliary lobe. This lobe varies from sturdy and short (about 1 1/2 times longer than wide) in BGR, kv 337 to slender and long (about 3 times longer than wide) in BGR, kv 339. It is followed by very narrow, slit-like fifth lateral saddle, which is situated within the inner third of the umbilical wall in both sutures. In BGR, kv 337 (Figure 25c) the saddle is halved by a tiny, tack-like, simple lobule. However, it is undivided in BGR, kv 339 (Figure 25a). There, the next following lobe-like structure is only recognizable as the third and last auxiliary lobe because of its large size that much exceeds that of the lobules of the fourth lateral saddle. The following third and last auxiliary lobe is sturdy and about half as large as the second auxiliary. It is triangular-shaped, markedly to distinctly inclined adventrally, and only slightly notched in both sutures. In BGR, kv 339 this lobe is situated hard at the umbilical seam. However, in BGR, kv 337 it is separated from that seam by the greater part of the sixth lateral saddle. This saddle is about three times wider than the third auxiliary lobe and is subdivided in two by a tiny, tack-like lobule. The fourth auxiliary lobe is not exposed either in these two sutures

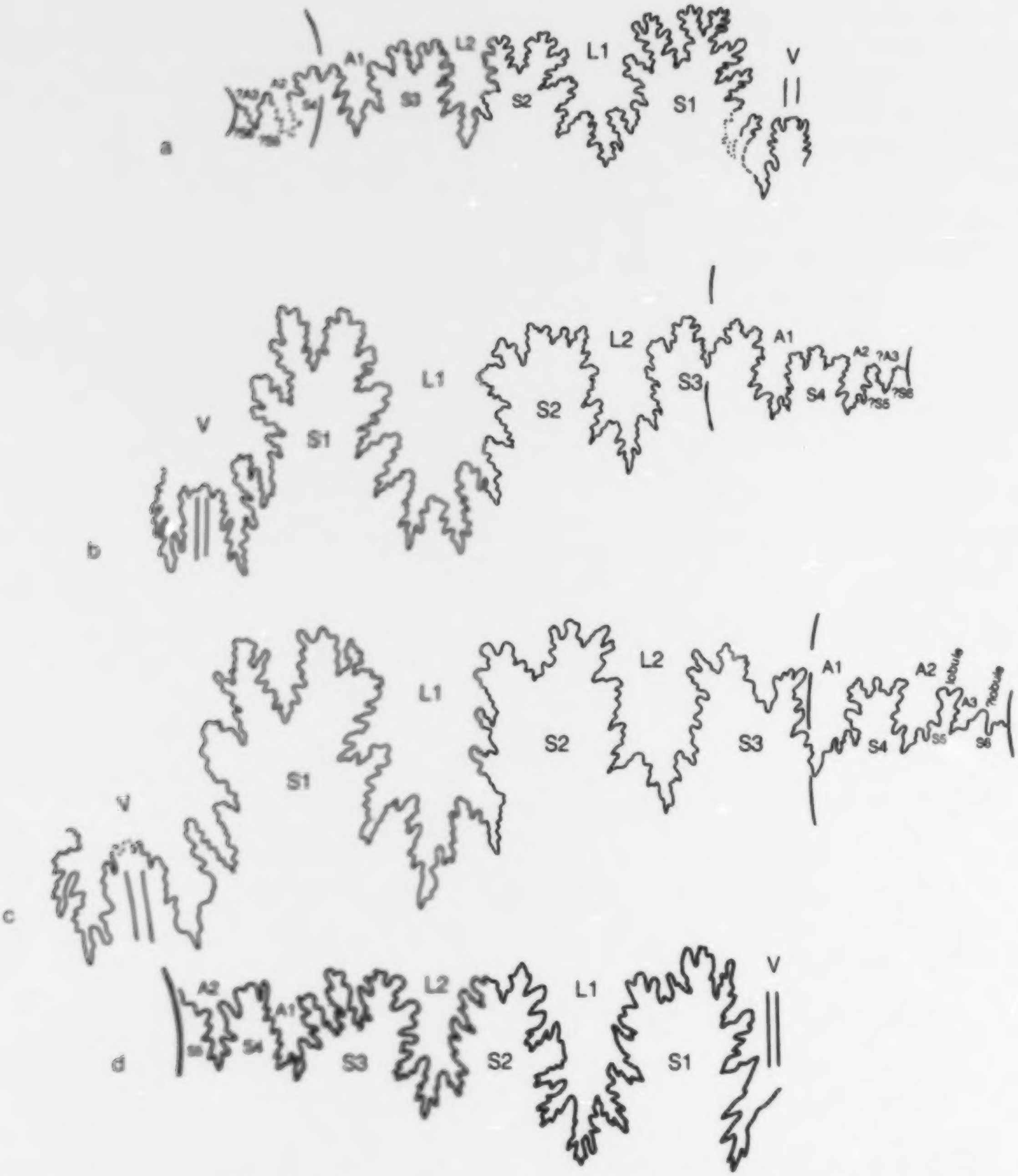

a
A1
A2
L2
S3
S2
L1
S1
V
b
V
S1
L1
S2
L2
S3
A1
A2
?A3
S4
?S5
?S6
c
V
S1
L1
S2
L2
S3
A1
A2
S4
lobule
A3
S5
lobule
S6
d
A2
A1
L2
L1
V
S5
S4
S3
S2
S1

Figure 25. Variability of adult external suture line of *Polyptychites keyserlingi* (Neumayr and Uhlig, 1881). **a.** Progressive variant, BGR, kv 339. Lindhorst, Northwest Germany. At the shell diameter of 85 mm; **b.** Conservative variant, BGR, kv 338. Bueckeburg-Jetenburg, Northwest Germany. At the whorl diameter (wh) of 24 mm; **c.** Progressive variant, BGR kv 337. Lindhorst, Northwest Germany. At the whorl diameter (wh) of 26 mm; **d.** Conservative variant. Reproduction of suture figured by Koenen (1902, Pl. II, fig. 4). Osterwald, Northwest Germany. All figures are approximately natural size.

or in any other known example of this advanced variant. Koenen (1909) did not illustrate the adumbilicalmost parts of the suture lines of any representatives of *P. keyserlingi* he did figure. However, the great width of space available for the second and third auxiliaries in his specimens and their comparison with the BGR specimens studied indicate the presence of a third auxiliary lobe in these specimens as well.

The above discussed morphological details of the progressive variant of the suture are rather variable and the same is true of all its other morphological details, except for the presence of three auxiliary lobes. For example, the sutures of BGR, kv 337 (Figure 25c), those of some other unfigured BGR specimens, and those of *P. k. arcuatus* (Koenen, 1909, Pl. XI, figs. 1, 3) are distinguished by their relatively more sturdy, more shallowly denticulated lobes and by a stronger crowding of auxiliary lobes on the umbilical wall. In these, as well as in other above discussed features, these sutures are distinctly transitional to those of the previously discussed morphologically and evolutionarily conservative variant. One could segregate them as the median variant instead of including them into the progressive variant because of the presence of three auxiliary lobes.

Other sutures of the morphologically and evolutionarily progressive variant are distinguished by their relatively more slender and longer, more deeply denticulated lobes separated by relatively wider, more deeply and richly denticulated saddles. Furthermore, as already mentioned, their first auxiliary lobe is situated at or near the top of the bulla and the fourth lateral saddle begins on the innermost part of the flank. These typical representatives of the variant are exemplified by those of BGR, kv 339 (Figure 25a) and *P. k. suessi* (Koenen, 1909, Pl. XII, figs. 2, 3). These most advanced external sutures known in the European representatives of *P. keyserlingi* are particularly similar to those of its Canadian representatives (compare Figure 47a). At the same time, these sutures are most closely similar to those of *P. hapkei* which appears to be a direct descendant of *P. keyserlingi*.

It should be pointed out in this connection that the figured type specimen of *P. keyserlingi* var. *suessi* is a relatively slender, relatively high-whorled and narrowly umbilicated shell with a reduced number of umbilical bullae (about 16) per whorl. It resembles closely the Canadian forms of the species (especially the more closely sculptured specimen GSC 77095; Pl. 32, fig. 2) also in these respects.

The orientation of the external suture lines of *P. keyserlingi* figured by Koenen (1909) is just as variable as its other morphological features. It may be subradially oriented in some forms (e.g. in *P. k.* var. *robustus*) while being distinctly ascendant throughout its inked in part in some others (e.g. *P. k. costellatus*). The latter suture appears to match closely that of the Canadian representative of the species. In yet other forms (e.g. *P. k.* var. *salchowi*) only the two lateral lobes are ascendant whilst all auxiliaries visible are descendant (or retractive). This suture is accordingly abruptly bent in the middle. Finally, the complete suture line of BGR, kv 337 (Figure 25c) is ascendant at 15° to 20° in its lateral part including the first auxiliary lobe. Then the suture rapidly bends over first into subradial orientation and still later (the second and third auxiliary lobes only) into a markedly (about 10°) descendant orientation.

The information on stratigraphic ranges of the above discussed "conservative" and "progressive" types of the suture line is scarce and inexact. The main reason is the lack of bed by bed collecting in the Jetenburg and Lindhorst clay pits, which have yielded the bulk of the *P. keyserlingi* material. These pits, which no longer exist, are known to have overlapped stratigraphically to a considerable extent. However, the Lindhorst section also includes younger *Polyptychites* Beds, which were not exposed at Jetenburg. Therefore, one would expect that many specimens of *P. keyserlingi* from the Lindhorst pit would be younger than those from the Jetenburg pit. The strong prevalence of the morphologically progressive suture line in the Lindhorst-derived specimens of *P. keyserlingi* present in BGR collections should, therefore, be significant. The prevalence of the "morphologically conservative" suture lines in the studied specimens from Jetenburg pit supports this conclusion. The idea that the "morphologically progressive" suture line is prevalent in younger representatives of *P. keyserlingi* while the "morphologically conservative" suture is prevalent in its older representatives is also supported by the type material of the species which is from the basal part of *Polyptychites*-Beds. The medium-sized cotype, which has a morphologically conservative suture, is from stratigraphically old Osterwald locality. A second specimen from Osterwald reproduced in Figure 25d also has a conservative adult suture line.

From this evidence, the writers infer that the "morphologically progressive" suture line is also evolutionarily progressive.

The sculpture is, as a rule, relatively coarse and its coarseness increases with age. The primary ribs are transformed into typical bullae in an early growth stage, at shell diameters of 20 to 30 mm. Similarly to the other sculptural elements, the bullae become progressively coarser during ontogeny and the distances between them increase somewhat. The number of bullae decreases accordingly from 19 to 20 to some 17 to 18 in the adult state. In the progressive variants their number per whorl decreases to 13-15 in the adults. The bullae become higher and higher at the same time and commonly more spinose.

The primary ribs and bullae extend onto the umbilical wall where they end either at or very close to the umbilical seam. These extensions of the primary ribs are oriented approximately radially in the early growth stages. However, they acquire a forward bend when the bullae appear for the first time and this bend increases gradually in the course of ontogeny. On the living chamber of progressive variants these extensions of bullae form an angle of about 50° with the umbilical seam.

The number of secondary ribs and the bundling habit differ from one ontogenetic stage to another. Juvenile shells with diameters less than 4 to 8 mm do not exhibit any sculpture (BGR, kv 267). Thereafter appear swollen primary ribs which merge into about twice as many secondary ribs without any obvious bundling habit. Then a very short sculptural stage with irregular and quasibidichotomous bundles is followed by more prolonged stage with trivirgatitpartitous bundles (BGR, kv 268). At shell diameters of 40 to 50 mm this sculpture grades into that of the subadult stage. This is achieved via an increase in the number of secondaries per bundle (Pl. 6, figs. 1-4). The subadult sculpture is dominated by quadrivirgatitpartitous rib bundles. These bundles were defined by Kemper (1978) as oligoptychous as the anterior and posterior dichotomous elements branch directly from the bullae. This bundling habit is, therefore, not exactly virgatoptychous. Trivirgatitpartitous bundles, and also bundles with five secondary ribs, which can be named the true polyptychous bundles (see p. 15 and Figure 9) are rarely intercalated with the oligoptychous bundles. This subadult sculptural stage has the greatest number of secondary ribs per bundle. The number of secondaries decreases in the following adult stage. This stage is again dominated by approximately trivirgatitpartitous bundles with intercalated ribs between them. The adult sculptural stage of less progressive specimens is also characterized by a distinctly increased variability and irregularity of the sculpture.

Affinities and differences. This species of the lower and middle *Polyptychites*-Beds is one of the principal form groups of the genus. Its palaeogeographic range is exceptionally wide as it has been found in Middle and Northwest Europe, the Russian Platform, Novaya Zemlia, Spitsbergen, Greenland, Northwest Siberia and Arctic Canada (Sverdrup Basin). A closely related form was even found in the Tethyan Realm (i.e. in Southeastern France; Thieuloy, 1977, Pl. 6, fig. 11). The species differs from other representatives of the *Polyptychites keyserlingi* species group primarily in its broader whorls, which increase more strongly in width in the course of ontogeny.

P. keyserlingi is, as already mentioned, a typical representative of *Polyptychites*. Several other species of *Polyptychites* acquire adult growth stages that are very similar to those of *P. keyserlingi*. These homeomorphies complicate extraordinarily the reliable identification of such taxa. These uncertainties are indicated by question marks in the list of synonyms of *P. keyserlingi*. It is particularly difficult to differentiate this species from the tuberculate variant of *P. michalskii*.

Polyptychites ascendens Koenen 1902

Pl. 5, figs. 3, 5; Pl. 7, fig. 2; Figure 26a, b.

*1902 *Polyptychites ascendens* Koenen, p. 410-412, Text-fig. 2 (?Pl. 55, figs. 10a, b).
non 1909 *Polyptychites ascendens* Koenen, p. 81, 82, Pl. 32, figs. 2, 3.

Holotype. Specimen figured by Koenen, 1902, Fig. 2, which is preserved in GIG collections. Its plaster cast is preserved in the BGR collections, Hannover, No. kv 272.

Locus typicus. Bueckeburg-Jetenburg.

Stratum typicum. (lower?) *Polyptychites*-Beds (= middle part of the lower Valanginian).

Material. 18 specimens from the localities Bueckeburg-Jetenburg and Lindhorst.

Diagnosis. Small species of *Polyptychites* with slender to at the most moderately wide shell and a narrow to moderately narrow umbilicus. Sculpture is refined. Bullae are fine but develop early (at about 30 mm shell diameter) out of primary ribs. Adult external suture line is like that of *Polyptychites oerlinghusanus*.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
BGR, kv 271	53	13(25)	18(34)	22(42)	—	26?
BGR, kv 94	59	18(30)	18(30)	23(39)	20?	27?
BGR, kv 97	71	21(30)	22(31)	27(38)	25	32
BGR, kv 95	61	18(29)	19(32)	24(39)	21?	26?

Description. The holotype was comprehensively described by Koenen (1902). It is obliquely deformed, which makes it impossible to evaluate the thickness of the shell. The authors were able to study better preserved material and so are able to improve the description of the species. A tendency toward deformation is also pronounced in our material. The shell of this species must have been especially thin. Consequently, it had less strength than the shell of other *Polyptychites* species.

P. ascendens developed out of the more finely ribbed variants of *P. pavlowi* via a decrease in the width of the umbilicus. There exist transitional forms which are difficult to assign to one or the other of these two species. The diameter of adult shells fluctuates between 60 and 70 mm and the width of the umbilicus fluctuates between 25 and 30 per cent. The whorls are low and somewhat wider than high. The increase of the whorl's width is insignificant (Pl. 7, fig. 2B). In advanced growth stages the whorls commonly become somewhat more narrow, instead of (as for example in *P. keyserlingi*) becoming thicker. The whorl section varies from a regularly arched (Roman arch; Pl. 5, fig. 3B) shape to one with less convex flanks and a somewhat more narrow adventral arching.

The umbilical shoulder is broadly rounded. The umbilical wall is relatively gently inclined. It is pronouncedly convex on the early growth stages but this convexity decreases considerably on the penultimate whorl and in the adult growth stage. In spite of a pronounced rounding of the umbilical shoulder and a considerable degree of involution, the umbilicus appears to be step-like rather than funnel-like. The length of the living chamber is at least one whorl.

The adult external suture line, which is best visible in specimen BGR, kv 95 (Figures 26a, b), is closely simi-

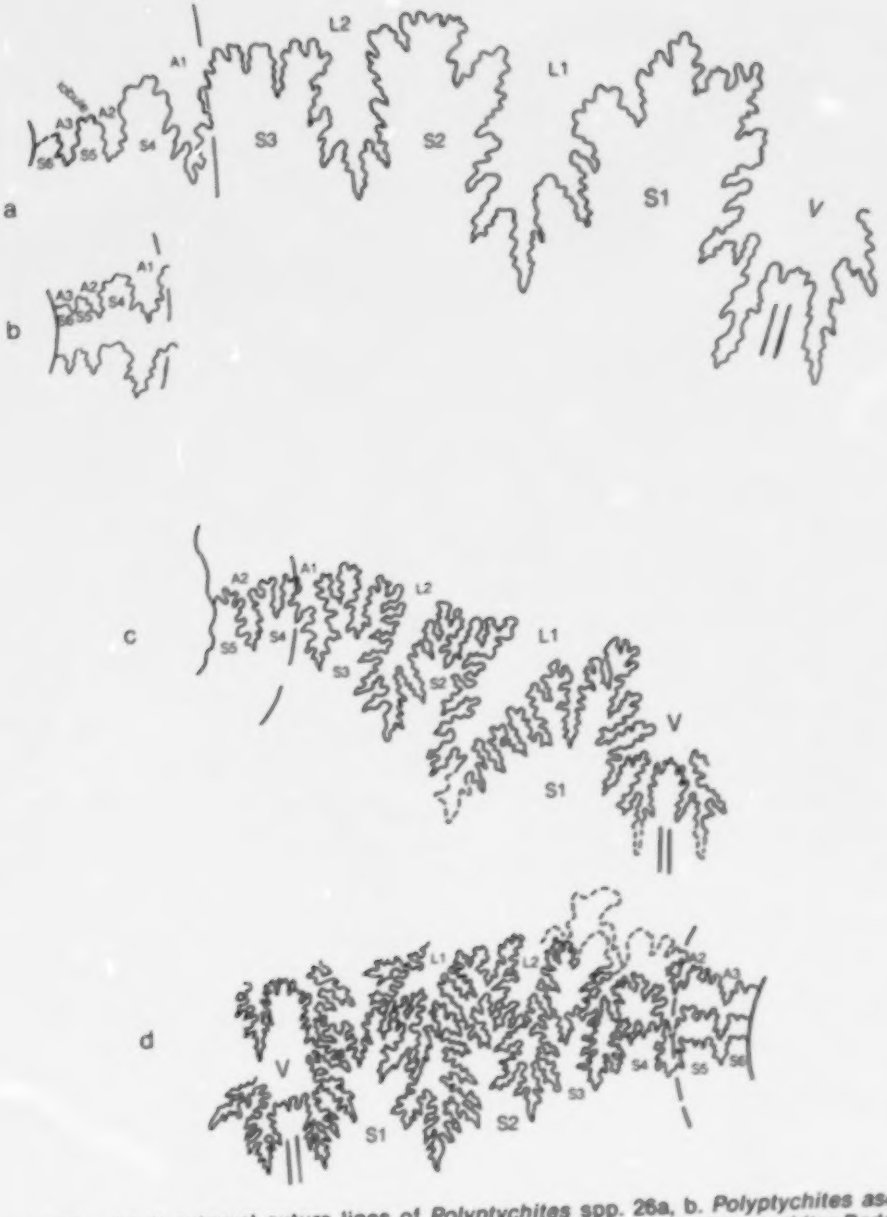


Figure 26. Adult external suture lines of *Polyptychites* spp. 26a, b. *Polyptychites ascendens* Koenen, BGR, kv 95. Bueckeburg-Jetenburg, Northwest Germany. Lower *Polyptychites*-Beds, middle lower Valanginian. **a.** Complete suture at the whorl height (wh) of 16 mm, x 6.6. **b.** Umbilical part of the suture at the whorl height (wh) of 24 mm, x 8.8. **c.** *Polyptychites clarkei* Koenen, BGR, kv 277. Lindhorst, Northwest Germany. *Polyptychites*-Beds, lower Valanginian. Typical variant of the suture with only two auxiliary lobes. At the whorl height (wh) of 47 mm, x 1. **d.** *Polyptychites* aff. *saxonicus* n. sp. BGR, kv 110. Twiehausen, Northwest Germany. Lower upper Valanginian. Morphologically and presumably evolutionarily advanced form of the species. Three sutures at the whorl height (wh) of 55 mm (compare Pl. 12, fig. 1), x 1.

lar to that of *Polyptychites oerlinghusanus* in the shape and spacing of its lobes and saddles and the degree of denticulation of its elements. Like that of *P. oerlinghusanus* again, it is distinctly and approximately evenly ascendant in its lateral part (including the third lateral saddle). Then the suture rapidly becomes subradially oriented over the first auxiliary lobe before gradually swinging into a distinctly descendant orientation which continues to increase to the umbilical seam. Like the suture line of *P. oerlinghusanus* again, that of *P. ascendens* has three auxiliary lobes in addition to the two lateral lobes. The first auxiliary lobe is situated at or near the crest of the umbilical shoulder. The second auxiliary, which is a small and sturdy, triangular-shaped structure, occupies the middle of the umbilical wall. The third, tiny and tack-shaped to but slightly denticulated auxiliary occurs next to the umbilical seam. The fifth lateral saddle preceding the third auxiliary is very narrow. However, in the adult suture line at least (Figure 26a), it is subdivided in two by a tiny lobule, which attests to the nature of the third auxiliary lobe that follows it.

In spite of its being shallowly and sparsely denticulated, the adult external suture line of *P. ascendens* is better referred to the morphologically advanced type because of the presence of three auxiliary lobes, the first of which is situated on the umbilical shoulder. The relatively slender, parallel-flanked shape of the lateral lobes combined with their relatively wide spacing (except for the fifth lateral saddle, all intervening saddles are considerably wider than the preceding lobes) points in the same direction.

Because of the evident derivation of *P. ascendens* from *P. pavlowi*, the close resemblance of its external suture line to that of *P. oerlinghusanus* must be a matter of homoeomorphy only.

The sculpture is relatively fine and dense (Pl. 5, fig. 3). Slender primary ribs become transformed into fine but typical bullae at shell diameters of about 30 mm. On the penultimate and ultimate whorls the bullae number 20 or somewhat more (BGR, kv 95: 21; BGR, kv 94: 20; BGR, kv 97: 23, holotype: 20). Their number only falls below 20 in extreme variants (BGR, kv 271 about 19?). Primary ribs and bullae are bent forward (comma-like) on the umbilical wall from their first appearance and remain so throughout ontogeny. On the early whorls they extend to the umbilical seam. However, in adults they disappear already on the inner third of the umbilical wall. In the holotype and specimens BGR, kv 94 and kv 271 the bullae form narrow and somewhat radially extended elevations. However, they are less prominent in other representatives of the species.

The ornamentation varies from one ontogenetic stage to another. It was not possible to observe it on the early growth stages. It was only possible to establish the presence of a prolonged growth stage with trivigatitpartitous rib bundles. This stage extends to shell diameters of 40 to 50 mm. Then follows a more or less short sculptural stage with irregularly bidichotomous sculpture (Pl. 5, fig. 5A; Pl. 7, fig. 2A). In the holotype quasi-quadrivirgatitpartitous bundles arise via addorsal migration of the anterior dichotomous element. Supplementary subdivision of the anterior branch of the bundle or the appearance of intercalated secondaries results in the appearance of bundles with five secondary ribs, which represent the highest level of sculptural development in this species (Pl. 5, fig. 5A). The number of secondaries per bundle decreases again in the adult growth stage. Here the trivirgatitpartitous bundles alternate again with the irregularly bidichotomous bundles. The loss of a regular pattern of rib bundling is, thus, present also in the adult stage of this species.

Affinities and differences. The species is so far known only from Northwest Germany, where there are transitional forms from the ancestral species of *P. pavlowi*. From this species *P. ascendens* differs particularly in the narrower umbilicus, the lesser width of the whorls, an earlier appearance of typical bullae and the presence of three auxiliary lobes in the adult suture line. Its sculpture is finer and denser in comparison with that of other species of the *P. keyserlingi* species group. *P. michalskii* possesses a similarly fine sculpture. However, this species lacks bullae (except, perhaps, in the adult growth stage). Furthermore, the whorls of *P. michalskii* are considerably thicker and exhibit a tendency toward flattening of the venter. Finally, its external suture line is said to have only two auxiliary lobes.

P. ascendens differs from representatives of the subgenus *Siberiptychites*, including the superficially similar *S. stubendorffi* (Schmidt), in an entirely different bundling habit of the intermediate whorls, absence of constrictions, and early appearance of umbilical bullae. The sculpture is dominated by an alternation of bidichotomous, posteriorly virgatotome (i.e. the subradially oriented posterior secondary rib throws off one, two or three tertiary ribs directed backward) and anteriorly virgatotome (i.e. the anterior secondary rib throws off one, two or three tertiary ribs directed forward as in *ramulicosta*) bundles. Bidichotomous bundles become prevalent later. The trivirgatitpartitous bundles are either rare or completely absent in these growth stages. *P. ascendens* belongs accordingly to the *P. ramulicosta* species group according to its sculpture. However, its suture line is more advanced (it has 3 lobes on the flank) than those of all of its contemporaries and relatives.

Polyptychites ramulicosta Pavlow 1892

Pl. 8, fig. 1; Pl. 11, fig. 2; Pl. 12, fig. 3

1892	*Olcostephanus (Polyptychites) ramulicosta* Pavlow in Pavlow and Lamplugh, p. 481, Pl. 8, fig.10a, 10b; Pl. 15, figs. 6a-6c.
1902	*Olcostephanus ramulicosta* Bogoslovsky, p. 135, Pl. 15, figs. 5a, 5b.
?1960	*Polyptychites* aff. *quadrifidus* Klimova, p. 173, 174 (pars), Pl. 21, figs. 5, 7, 8 (non fig. 6).

Lectotype. Selected herein, the original to Pavlow in Pavlow and Lamplugh, 1892, Pl. 15, figs. 6a, 6b (?preserved in the Scarborough Museum, Yorkshire, England).

Locus typicus. Speeton, Yorkshire, Great Britain.

Stratum typicum. Originally designated (Pavlow and Lamplugh, l. cit.) as: "Partie superior du sous étage Aquilonien." Actually derived from Bed D2 to D4, Valanginian (Spath, 1924, p. 75).

Material. Two well preserved specimens from Northwest Germany (Lindhorst). It is doubtful whether the three morphologically similar but badly preserved, laterally deformed specimens described by Klimova (1960, see in the synonymy) from boreholes in Northwest Siberia (Tobol'sk 3-R, Vikulov 1-R) belong to this species. Except for the specimen described and figured by Bogoslovsky (1902; see in the synonymy), all records of *P. ramulicosta* from the European Arctic and northern U.S.S.R. are believed to be erroneous and to represent *Siberiptychites (Siberiptychites) stubendorffi*.

Diagnosis. Small species with a narrow umbilicus. The sculpture is fine and dense; it consists of predominantly quasi-trivirgatitpartitous rib bundles to a diameter of at least 60 mm. Bullae are also very numerous and fine but have a typical appearance and appear in the early stages of ontogeny. The adult external suture line has only two auxiliary lobes.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
BGR, kv 301	49	11(22)	16(32)	22(45)	18	24

Description. The shell of BGR, kv 301 is perfectly preserved to a diameter of 55 mm (Pl. 8, fig. 1A, B). Only a fragment of its more advanced whorls is preserved (Pl. 8, fig. 1C). It was not possible to measure its adult size but it is assumed to be in the order of 90 mm.

The flanks of early whorls are only slightly convex and connected with each other by a broad and obtuse ventral arch. A rounded umbilical shoulder connects the flanks witn a low and convex umbilical wall. The umbilicus is rather narrow and funnel-like rather than step-like. About 70 per cent of the preceding whorls are enclosed by successive whorls. The taxonomically doubtful West Siberian material is compressed and does not permit any conclusions about its shape and proportions.

The suture line is not visible in either of the Northwest German specimens. However, the holotype exposes a well preserved and complete, presumably adult external suture line (Pavlow, in Pavlow and Lamplugh, 1892, p. 480, Pl. XV, fig. 6a) that is characterized by very slender and long, subparallel-sided, deeply and fairly complexly denticulated lobes (including the auxiliaries), that resemble closely those of advanced representatives of *P. ascendens* (e.g. Koenen, 1909, Pl. XXXIII, fig. 3; this paper, Figures 26a, b) and *P. keyserlingi* var. *suessi* (Koenen, 1909, Pl. XII, fig. 3). However, this suture has only two auxiliary lobes and so represents yet another, presumably specialized variant of the conservative polyptychitinid suture line.

The sculpture of specimen kv 301 (Pl. 8, fig. 1) is fine and dense. The bullae develop from the primary ribs very early in ontogeny. They appear at a shell diameter of about 20 mm and acquire a comma-like bend. The bullae are slender but typically developed. There are 24 bullae on the whorl that ends at a shell diameter of 50 mm. The bullae extend onto the umbilical wall where they peter out at about its middle. Quasi-trivirgatitpartitous (i.e. bimonotom sensu Kemper, 1978) rib bundles start from the bullae as is characteristic of the early growth stages of the older species of *Polyptychites*. This bundling habit is ontogenetically longlasting. It is retained to a shell diameter of about 60 mm. Only a few bundles with a greater number of secondaries occur at a shell diameter of 70 mm. These bundles represent the highest level of sculptural differentiation in the species. This increase in the number of secondaries is achieved by an intercalation of an additional dichotomous secondary, which is either not connected with the bulla or is only indistinctly connected with it. Thereafter occurs a reduction of the number of secondary ribs characteristic of the adult growth stage. This results in the restoration of quasi-trivirgatitpartitous bundles, which are now more irregularly developed than before.

Specimen BGR, kv 319 is a morphologically conservative variant, the ontogenetic development of which is observable. It has fasciculate rib bundles to a whorl diameter of 13 mm (Pl. 12, fig. 3C). This stage is followed by a short sculptural stage (about 1/3 of a whorl long) with bidichotomous bundles. This stage is followed, in turn, by the one with a prevalent quasi-trivirgatitpartitous sculpture.

Affinities and differences. Judging by its sculpture, whorl shape and stratigraphic position, *P. ramulicosta* could have evolved out of *P. ascendens* via a narrowing of the umbilicus and an increase in the density of the sculpture. However, its distinctly more conservative external suture line is against this interpretation. It is rather suggestive, instead, of *P. ramulicosta* being a parallel but independent offshoot of the *P. pavlowi* species group. This is also suggested by the fact that its sculpture retains the more primitive quasi-trivirgatitpartitous bundling habit, except for a few bundles. The prevalence of a quasi-trivirgatitpartitous bundling habit in combination with a very dense sculpture, very narrow umbilicus, relatively slender shell and a conservative but slender-lobed external suture line typifies *P. ramulicosta*. This combination of morphological features permits its easy differentiation from other *Polyptychites* species and from the homoeomorphically similar *Siberiptychites (Siberiptychites) stubendorffi*.

Polyptychites aff. *P. keyserlingi* (Neumayr and Uhlig 1881)

Pl. 7, figs. 4, 5.

?1962 *Polyptychites undulatocostatus* var. *multitudinis* Voronets, p. 77, Pl. 41, figs. 2a, 2b.

Material. 9 specimens from the *Polyptychites*-Beds (upper lower Valanginian) of Northwest Germany. Localities Bueckeburg-Jetenburg and Lindhorst.

Diagnosis. Small to medium-sized species with broad whorls and relatively wide umbilicus. Bundling habit approximately fasciculate and the ribs are moderately fine.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
BGR, kv 273	76	25(33%)	21(28)	30(39)	37(?)	45
BGR, kv 274	76	22(29%)	21(28)	33(43)	—	40
BGR, kv 275	81	26(32%)	25(31)	39(37)	37	40

Description of German material. The species is relatively small with the maximum known shell diameters being appreciably less than 100 mm. The whorls are considerably broader than high. Their largest width is situated at the level of the umbilical shoulder. The whorls are broadly rounded adventrally (Roman arch). The umbilical shoulder is rounded. The inner part of the umbilical wall is rather steep. In the adult stage the umbilical wall becomes more gently inclined and slightly convex. The relatively wide umbilicus (approximately 31 per cent) is funnel-like. The length of the living chamber is about one whorl.

The external suture line is conservative polyptychitinid with only two auxiliary lobes (in specimen BGR, kv 275). It seems to be most similar to that of *P. pavlowi* but the details are poorly preserved.

The sculpture is relatively fine. Its early ontogeny remains unknown because of an unfavorable preservation of all material studied. Typical and elevated bullae appear at least beginning with a shell diameter of about 30 mm. Specimen BGR, kv 273 (Pl. 7, fig. 5A) has 19 bullae on the last whorl and BGR, kv 274 (Pl. 7, fig. 4) has 17. The bullae extend onto the umbilical wall where they extend to the umbilical seam at least in the early and intermediate growth stages. They have a forward directed comma-like bend already on early ontogenetic stages (beginning with whorl diameters of 20 to 30 mm).

The ornamentation, which can be designated as almost olcostephanid, is very characteristic. Namely, most secondary ribs arise directly out of their bullae. They form approximately fasciculate bundles, especially on the last whorl. Additional (i.e. situated higher upflank) branchings of the anterior and posterior secondaries of a bundle occur only rarely. Such branchings indicate that the rib bundle is basically polyptychitinid and not olcostephanid. This becomes even more obvious when one considers the penultimate whorl of BGR, kv 274 (Pl. 7, fig. 4) where the ornament remains obviously polyptychitinid to a shell diameter of about 65 mm. On the early half of its last preserved whorl there are 4 to 5 secondaries per bundle. The bundles consist of a dichotomously branching anterior rib and a trivirgatitpartitous posterior element. An addorsal migration of the anterior dichotomous element may result in the emergence of an almost virgatitpartitous arrangement of 4 to 5 secondary ribs. This actually happens sometimes in this specimen. The addorsal displacement of splitting points is even stronger expressed on the anterior half of the last preserved whorl of BGR, kv 274, which results in the development of quasi-fasciculate bundles in its adult growth stage.

Affinities and differences. The species represents a particular and rather peculiar evolutionary lineage of the genus, which develops via a palingenetic modus an almost olcostephanid rib bundle. The similarities with the genus *Olcostephanus* are, however, caused only by homeomorphy as the earliest known representatives of *Olcostephanus* Neumayr are older. Furthermore, no transitional forms are known to connect the two.

The shell shape and proportions of *P.* aff. *keyserlingi* resemble those of the *P. keyserlingi* species group more than they do those of *P. multicostatus*. However, the peculiar development of its sculpture is so similar to that of *P. multicostatus* as to suggest their close affinity. The two differ in the shell shape, as that of *P. multicostatus* tends to possess subparallel flanks. *P.* aff. *keyserlingi* may be a connecting link between these two species groups.

The principal difference of *P.* aff. *keyserlingi* from other *Polyptychites* species consists of a quasifasciculate arrangement of its fine and closely spaced secondary ribs, at least in the adult representatives. The species has been found only in Northwest Germany and questionably in the Lena-Anabar Region of Northern Siberia.

Polyptychites multicostatus Koenen 1909

Pl. 8, figs. 2-4; Pl. 9, figs. 1, 2; Figures 27-30.

?1902	*Olcostephanus* sp. indet. C. Bogoslovsky, p. 141, Pl. 18, figs. 3a, b.
1906	*Olcostephanus (Polyptychites) ramulicosta* Danford, Pl. 11, figs. 3, 3a.
*1909	*Polyptychites multicostatus* Koenen, p. 83-85, Pl. 23, figs. 1, 2.
?1909	*Polyptychites compositus* Koenen, p. 55-57, Pl. 23, figs. 3, 4.
1909	*Polyptychites longelobatus* Koenen, p. 74-76, Pl. 29, figs. 1, 2.
1909	*Polyptychites denticulatus* Koenen, p. 77-79, Pl. 30, figs. 1, 2.
1909	*Polyptychites kittli* Koenen, p. 79-81, Pl. 31, figs. 1, 2.
1909	*Polyptychites plicatilis* Koenen, p. 85-87, Pl. 32, figs. 1, 4.

Holotype. The specimen figured by Koenen (1909) in Pl. 23, figs. 1, 2 by monotypy. In GIG collections, No. 410-27.

Locus typicus. Lindhorst.

Stratum typicum. Polyptychites-Beds (Lower Valanginian). Exact horizon unknown.

Material. In addition to the originals of figured specimens listed in the synonymy of *P. multicostatus*, 27 specimens in paleontological collections of BGR from the localities Bueckeburg-Jetenburg and Lindhorst.

Diagnosis. A medium-sized *Polyptychites* with relatively slender whorls. The whorl's width is, as a rule, either only slightly greater than the height or equals it. Only in the adult growth stage of morphologically conservative specimens is the width distinctly greater than the height. The flanks are only feebly convex and may be subparallel in the extreme forms. The sculpture is relatively dense and fine. The subdivision points of tertiary ribs are mostly situated very low on the flank (i.e. addorsally). This results in a partly quasi-fasciculate appearance of rib bundles. The adult external suture line has slender, deeply and richly denticulated lobes and saddles similar to those of *Polyptychites saxonicus* and *P. tethyale* but with distinctly more sturdy and thicker stemmed lobes. The third auxiliary lobe and the fifth lateral saddle are imperfectly developed.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
BGR, kv 105 (Slender variant)	96	22(23)	32(33)	42(44)	33	42
BGR, kv 107	106	27(25)	34(32)	45(42)	36	—
BGR, kv 98	112	31(28)	35(31)	46(41)	—	—
BGR, kv 99 (Thick variant)	106	29(27)	35(33)	44(41)	41	48(?)
BGR, kv 104 (Thick variant)	67	17(25)	22(33)	28(42)	24	35(?)

Description. The holotype was comprehensively described by Koenen (1909). The species is medium-sized (shell diameter up to about 110 mm) and relatively slender. The ontogenetic development of slender whorls follows a proterogenetic mode. The whorls of an intermediate growth stage with shell diameter of about 40 mm, which are visible in BGR, kv 107 (Pl. 8, fig. 4), appear to be slender and high in spite of their ratio wh = wth. The ratio wh > wth was not observed in the material studied. The slenderness of the whorls is therefore relative, as for example in comparison with the *keyserlingi* species group. The width of the whorls becomes relatively greater in subadult and adult growth stages.

In addition to the relatively small width of the whorls, the species is remarkable because of the insignificant convexity of its flanks. This is most pronounced in the early growth stages and decreases with growth so that the flanks may appear subparallel (e.g. in BGR, kv 105). This development follows the proterogenetic mode. The greatest width of the whorl remains, nevertheless, at the level of the umbilical shoulder. Depending on the orientation of the flanks and the width of the whorl, the shape of the venter fluctuates from a broadly rounded (BGR, kv 99, and kv 104; Pl. 8, fig. 3B) through a narrowly rounded oval (BGR, kv 107; Pl. 8, fig. 4B or BGR, kv 100) to a gentle arch confined between ventrolateral "angularities". The latter shape occurs in forms with subparallel flanks (e.g. BGR, kv 105).

The umbilical shoulder is broadly rounded and merges imperceptibly in the umbilical wall. The two form an inseparable element of the whorl's cross-section. A steep orientation of the wall occurs only in the proximity of the seam in some specimens (e.g. BGR, kv 105). In spite of a broad rounding of the umbilical shoulder and a relatively great degree of involution (about 80 per cent), the umbilicus appears to be step-like rather than funnel-like. The living chamber occupies approximately the length of one whorl.

The adult external suture lines (presumably those of the adult penultimate whorl; BGR, kv 324, kv 323, kv 105 (Figure 28); BGR, kv 102 (Figure 27); BGR, kv 343; the holotype (Koenen, 1909, Pl. XXIII, figs. 1, 2) and the original of *P.* "*longelobatus*" (Koenen, 1909, Pl. XXIX, figs. 1,2)) were studied in six well preserved specimens from Jetenburg and Lindhorst. So far as is known, these suture lines are rather uniform morphologically. They are exemplified by the sutures of the specimens BGR, kv 102 (Figure 27) and BGR, kv 105 (Figure 28). The sutures of the holotype and of the original of *P.* "*longelobatus*" do not expose the adumbilical parts and so are difficult to evaluate from the figures alone. However, their figured parts conform closely to the equivalent parts of other, completely exposed, adult sutures described below.

Generally speaking, the adult external suture lines of *P. multicostatus* differ strongly from the "morphologically conservative" sutures of *Polyptychites* ex gr. *pavlowi-keyserlingi* in their much greater complexity and the presence of an underdeveloped third auxiliary lobe (Figures 27, 28). At the same time they differ markedly from the morphologically more advanced sutures of some other representatives of *P. pavlowi-keyserlingi* species group (e.g. *P. keyserlingi* var. *suessi* Koenen) and *P.* ex gr. *hapkei* n. sp., that exhibit this third, sometimes similarly underdeveloped (e.g. Figures 21, 23, 25c, 26) auxiliary lobe, in a much greater length and slenderness of the lobes and lobules and in a much greater complexity and more deeply denticulated character of all their elements.

The lobes and saddles of *P. multicostatus* are complexly and deeply denticulated. The lobes are much longer, much more slender and, at the same time, considerably more irregular in shape than those of other above mentioned forms. They are also commonly slightly to clearly constricted at the top. In particular, both lateral lobes are usually irregularly trifid (Koenen, 1909, Pl. XXIII, fig. 1) and their terminal branches can be quite irregular. The same is commonly true of their lateral branches. The first order branches of their lobules are commonly long, wavering and subdivided into second order branches, which are, in turn, finely and closely incised (Pl. 8, figs. 2, 4A; Figures 27, 28).

The lateral part of the external suture lines of *P. multicostatus* is approximately straight and ascends at 35 to 40 degrees in relation to the corresponding radius (Figures 27, 28). Then it abruptly becomes slightly ascendant to subradially oriented at or near the umbilical shoulder in the interval between the first and second auxiliary lobes and remains so to the umbilical rim.

The first lateral lobe is only slightly shorter and smaller than the ventral lobe. The length and width of other lobes decrease more or less regularly all the way to the umbilical seam. They become at the same time less and less deeply and closely denticulated, although even the second auxiliary remains a moderately denticulated structure. Only the third auxiliary is an only simply laterally serrated and simply trifid structure.

The first auxiliary (see Koenen, 1909, Pl. XXIII, fig. 1; this paper, Pl. 8, figs. 2, 3A, 4A; Figures 27, 28) occurs either at the top of the umbilical bulla or somewhat lower on the lowermost part of the flank. A similar position of the first auxiliary lobe is seen in advanced forms of *P. keyserlingi* (i.e. *P. k.* var. *suessi* Koenen 1909). However, this similarity is due to homoeomorphy because of the presence of other more important morphological distinctions between the two (see earlier in this section and in Figures 27, 28).

The second auxiliary lobe that normally (see below for exceptions) occupies most or all of the outer half of the umbilical wall, is a relatively large, moderately deeply and complexly denticulated structure. This slender (2 to 3 times longer than wide) lobe is constricted at the top, which is always distinctly to markedly adventrally inclined. It is moderately to shallowly denticulated on the flanks and almost regularly (e.g. in BGR, kv 102; Figure 27) to irregularly (e.g. in BGR, kv 105; Figure 28) trifid. The terminal branches vary from long, slender and moderately deeply and complexly denticulated in BGR, kv 102 to fairly short and simply denticulated in BGR, kv 105. In the latter the second auxiliary lobe gradually moves adventrally on the last preserved one-third of the whorl until it is situated on the adumbilical flank of the umbilical shoulder in the last few preserved sutures (Figure 28b). Only the third and last auxiliary lobe, which is situated hard at the umbilical seam in all suitably preserved specimens studied, except for the oralmost few sutures of the specimen BGR, kv 105 (Figure 28b), is a sturdy (about two times longer than wide) and simply denticulated structure. It is only slightly notched on the flanks and the asymmetrically trifid termination. This auxiliary is recognizable as such only because of its relatively great size which comprises about one-half of that of the second auxiliary lobe and is much greater than the size of the lobules of the fourth lateral saddle (e.g. BGR, kv 102 and 105; Figures 27, 28). The exceptionally small width of the preceding fifth lateral saddle and the very feeble development of the median lobule within it (see below for further details) make the third auxiliary lobe look somewhat like an abnormally large lobule. However, this phenomenon is ascribed to the underdevelopment of this adumbilicalmost part of the external suture line. It is not uncommon in the intermediate and even adult external sutures of *Polyptychites* and other polyptychitinid genera. In this particular instance it may reflect the evolutionarily transitional character of the suture of *P. multicostatus* between the conservative sutures of *P.* ex gr. *pavlowi* on the one hand and the progressive sutures of *P.* ex gr. *saxonicus-tethyale* on the other. The latter (Figures 32a, c) invariably exhibit a normal development of the fifth lateral saddle and the third auxiliary lobe. These sutural elements are separated from the umbilical seam by the greater part of the sixth lateral saddle that is almost completely concealed in the presumably directly ancestral *P. multicostatus*, except again in the last few preserved sutures of specimen BGR, kv 105.

The saddles of all investigated sutures of *P. multicostatus* tend to be irregularly shaped because of an irregular shape of the flanking lobes. Generally speaking, the saddles are either about as wide as or only slightly wider than the preceding lobes but there is a distinct tendency for them to become relatively wider adumbilically between the first and fourth saddles. No part of the sixth lateral saddle is exposed, except in the few oralmost preserved suture lines of the specimen BGR, kv 105 where the outermost part of its top appears between the third auxiliary and the umbilical seam (Figure 28b).

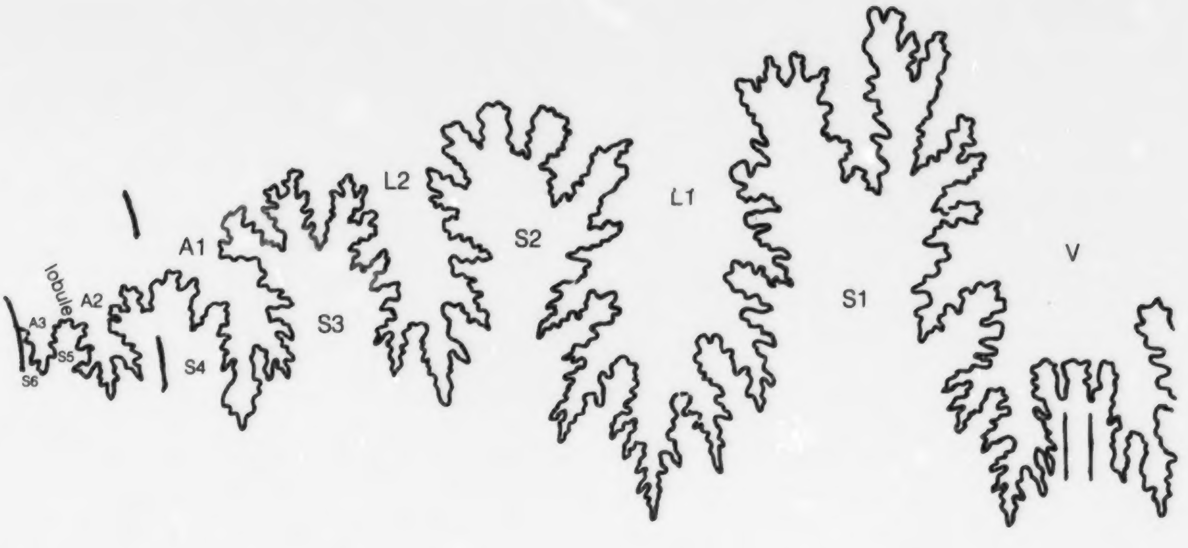
Most of the adjacent adult sutures (e.g. in kv 105; Figure 28b) are closely spaced (i.e. crowded) so that the tips of their lobes commonly touch the tops of saddles of the preceding sutures. However, no overlap of these sutures was observed. This attests to their advanced adult character.

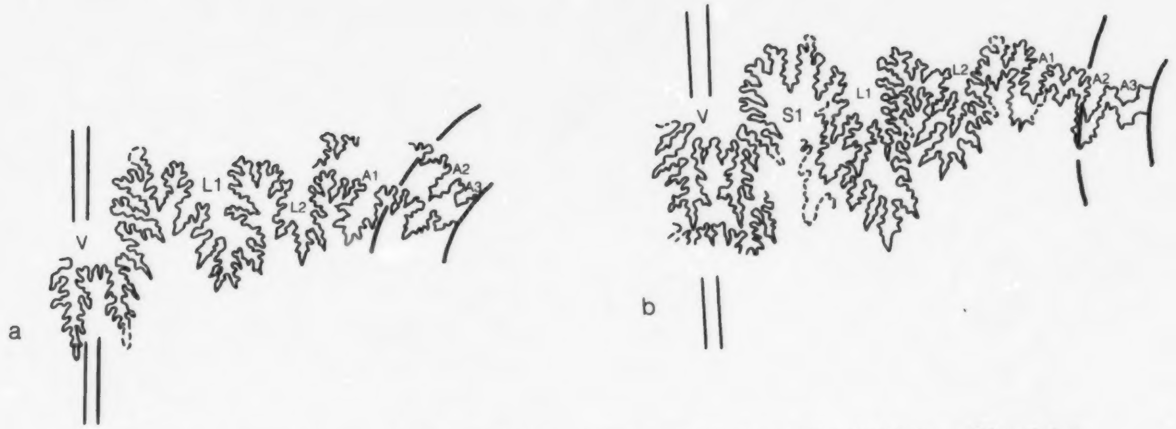
No sutures with relatively sturdy and shallowly denticulated, strongly adapically tapering lobes, such as occur in the holotype of *P. multicostatus* var. *denticulatus* Koenen (1902, Pl. XXX, figs. 1, 2) were seen in the material studied. Koenen's (l. cit.) form may be a pathological specimen.

The early adult external suture line of *P. multicostatus*, which was only observed in the specimen BGR, kv 107 (Pl. 8, figs. 4A, 4B) at an estimated shell diameter of about 45 mm, apparently has the same number and arrangement of lobes and saddles as the above described advanced adult sutures. It differs from the latter only in a relatively much less denticulated appearance of all its elements, including the apparently simple, roundtipped appearance of the second auxiliary lobe (the third auxiliary is not definitively visible), in the relatively increased size of the ventral and the first lateral lobes and in the adjacent suture lines being always narrowly separated from each other.

So far as is known, the adult external suture lines of *P. multicostatus* are closely similar in most characters only to the sutures of *P. clarkei* Koenen, *P. saxonicus* n. sp. (including *P.* aff. *saxonicus* n. sp.), *P. tethyale* n. sp. and, *P. orbitatus* Koenen 1902. The external suture line of these five species appears to represent the second type of *Polyptychites* suture line which is designated herewith as the *Polyptychites multicostatus* type.

The primary ribs are higher than the secondary ribs at whorl diameters of 30 to 40 mm (BGR, kv 197; Pl. 8, fig. 4A). Soon thereafter they become transformed into weakly bullate structures. The following numbers of these primary structures have been counted on the penultimate and ultimate whorls of our specimens; 19/19 in BGR, kv 99; 23/20 in BGR, kv 98; -/18 in BGR, kv 100 and 22/20 in BGR, kv 106. As indicated by these ratios, the

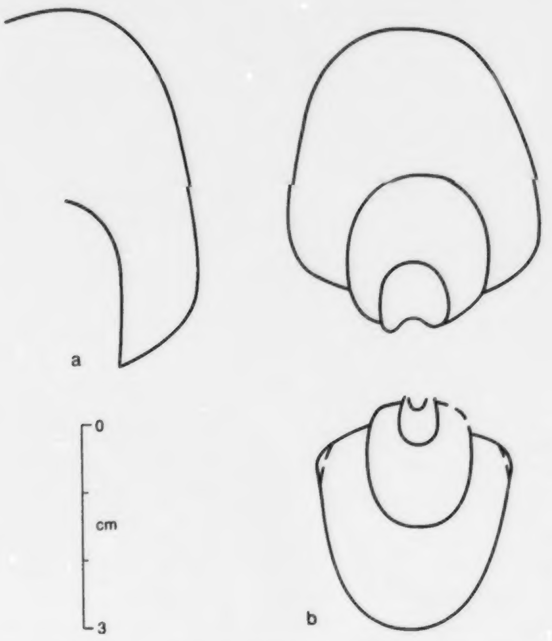


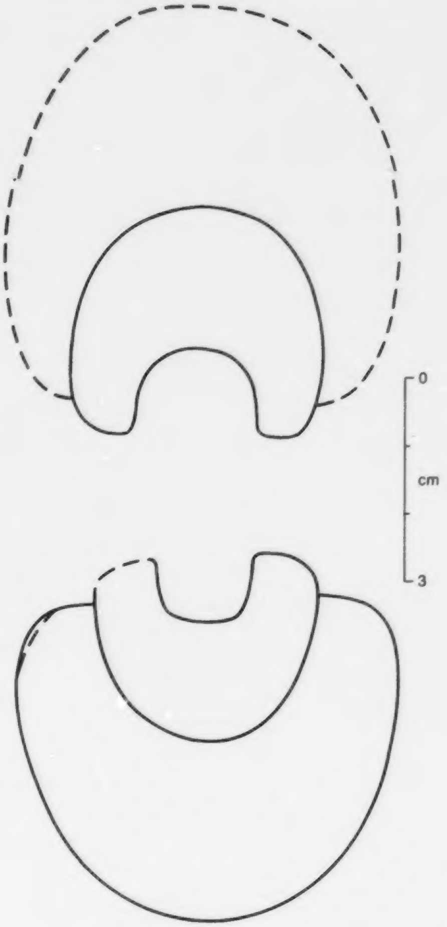


Figures 27 top, 28 bottom. Advanced adult external suture lines of *Polyptychites multicostatus* Koenen, 1902. 27. BGR, kv 102. Lindhorst, Northwest Germany. Suture observed on the ?adult penultimate whorl (wholly septate) at the whorl diameter of about 37 mm, x 2. Figure 28. BGR, kv 105. Bueckeburg-Jetenburg, Northwest Germany; **a**. Suture observed at the whorl height (wh) of about 38 mm and about one-third before the end of this wholly septate whorl, x 1; **b**. Two sutures at the oral end of the whorl at the whorl's height (wh) of about 44 m, x 1. Both specimens are from *Polyptychites*-Beds, upper lower Valanginian.

number of umbilical bullae decreases somewhat in the adult growth stage. The bullae extend onto the umbilical wall where they disappear approximately at the beginning of its inner third. These extensions are oriented approximately radially to the shell diameter of about 30 mm. However, they acquire a pronounced comma-like forward bend soon thereafter.

The sculpture is relatively fine and exhibits growth stage differences. That of the earliest stages is unknown. The secondary ribs are very fine at a shell diameter of about 30 mm (BGR, kv 107; Pl. 8, figs. 4A, 4B). At this stage dichotomous bundles alternate with quasi-trivirgatitpartitous bundles. Thereafter follows a growth stage where the number of secondary ribs increases to 5-6 per bundle. The tertiary ribs begin relatively low on the flank, either at about the middle of the flank or below it. This results in bundles having an almost fasciculate appearance. The similarity of this bundling habit with that of *Olcostephanus* is, however, only superficial in most representatives; it becomes more pronounced only in a few of the specimens studied (e.g. BGR, kv 106).





Figures 29 (above) and 30 (right). Three cross-sections of *Polyptychites multicostatus* Koenen, 1902. **a**. Specimen BGR, kv 322 from Lindhorst, Northwest Germany. *Polyptychites*-Beds, upper lower Valanginian. **b**. Specimen BGR, kv 323. The same locality and age as for the BGR, kv 322. Figure 30. Specimen BGR, kv 324. A thick variant from Bueckeburg-Jetenburg, Northwest Germany. The same age as for the other two specimens. The linear scale is valid for all three specimens.

A polyptychous mode of bundling is recognizable as a rule. At first occur bundles consisting seemingly of three secondary ribs, of which the anterior and the posterior split in two. The middle rib is not a secondary rib in the strict sense as it arises commonly out of the posterior secondary rib in the proximity of the bulla. This behaviour becomes more clearly expressed on the last whorl, as there occur more commonly obligoptychous bundles sensu Kemper (1978), which resemble the quadrivirgatit-partitous bundles (e.g. BGR, kv 103; Pl. 8, fig. 2). These bundles alternate commonly with irregularly bidichotomous rib bundles.

The sculpture becomes, as always, more irregular and coarser in the adult growth stage. In some specimens the ribs become somewhat lower on the addorsal (i.e. lower) parts of the flanks. The fact that in some specimens occur bifurcating intercalated ribs is phylogenetically important (e.g. BGR, kv 100 and kv 104; Pl. 8, fig. 3A). Through the addition of such bifurcating ribs, or through bifurcation of the median secondary, arise in a variant of our species rib bundles, which consist of 3 fairly regularly bifurcating secondary ribs ("*hapkei*-sculpture"). This development follows a palingenetic mode.

Affinities and differences. *P. multicostatus* is a species that is important for the understanding of the phylogeny of Polyptychitinae. It forms part of an evolutionary lineage which originates in the *P. pavlowi* species group and gives rise to the younger *Polyptychites*-species of the late early and early late Valanginian and thus also to *Prodichotomites* (Figure 11). The differences of *P. multicostatus* from those taxa, which possess a *hapkei*-like sculpture, consist first of all in the fact that the development of three secondary ribs in *P. multicostatus* only begins in the latest growth stages and that the point of their subdivision is situated relatively farther addorsally in most representatives. Furthermore, the somewhat similar external suture line has underdeveloped fifth lateral saddle and third auxiliary lobe. Finally there exist differences in the shell shape, which will be treated in the description of the offspring taxa. *P. multicostatus* differs from other younger species groups of *Polyptychites*, among other things, in the presence of fasciculate rib bundles. The development of quasi-fasciculate rib bundles in some variants produces certain similarities with the genus

Olcostephanus Neumayr, which are, however, purely homoeomorph in character.

The species group of *P. keyserlingi* is a lineage which parallels that of *P. multicostatus*. However, it differs from the latter in higher and coarser bullae and wider whorls, the flanks of which are pronouncedly convex. The two lineages also differ in other features, for example in the sculptural style and the morphology of the adult external suture line.

P. multicostatus is known only from Northwest Germany and eastern England (Speeton).

Polyptychites clarkei Koenen 1909

Pl. 29, figs. 1A, 1B; Figures 26c, 31, 32b.

*1909 *Polyptychites Clarkei* Koenen, p. 64, 65, Pl. 25, figs. 1, 2.
1909 *Polyptychites Stolleyi* Koenen, p. 67, 68; Pl. 26, figs. 1, 2.
?1909 *Polyptychites Kokeni* Koenen, p. 71-73; Pl. 27, figs. 1, 2.
1909 *Polyptychites Rinnei* Koenen, p. 70, 71; Pl. 28, figs. 1, 2.

Holotype. The specimen figured by Koenen (1909, Pl. 25, fig. 1, 2) is the holotype of *P. clarkei* through monotypy. It is in GIG collections, Type Cat. No. 410-31.

Locus typicus. Lindhorst.

Stratum typicum. *Polyptychites*-Beds (lower Valanginian). Exact horizon unknown.

Material. 13 specimens from Lindhorst (BGR Hannover) in addition to the previously figured specimens listed in the synonymy.

Diagnosis. A medium-sized to large representative of the genus. The ontogenetically advanced whorls are high, relatively narrow and with only feebly convex flanks. The height of the whorl increases only slowly, which results in a correspondingly shallow umbilicus. The umbilical shoulder and the umbilical wall are shallowly rounded (or low rounded). The sculpture of the penultimate and ultimate whorls is coarse and has only four secondary ribs per bundle. The bundling habit is predominantly of *P. keyserlingi* type. The slender-lobed, richly and deeply denticulated adult external suture line differs from the similar suture of *P. multicostatus* in a prevalent presense of only two auxiliary lobes.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
kv 86	130	35(27)	43(33)	53(41)	46	57
kv 87	134	40(30)	39(29)	55(41)	54	63
kv 88	134	36(27)	46(34)	52(39)	52	61
kv 276	167	44(26)	59(35)	64(38)	65	—
kv 277	147	43(29)	46(31)	57(39)	54	64

Description. It is not necessary to refigure the original material of the species in this paper as several perfect figures of it are available in the literature (e.g. Koenen, 1909, Pls. 25-28). Some of the specimens studied (e.g. BGR, kv 86-88) are excellently preserved (e.g. Pl. 29, fig. 1). The species is quite large, with shell diameters of at least 140 to 200 mm. In spite of the whorls being always broader than high, their relative height increases in the course of ontogeny. This development is coupled with a decrease in convexity of the flanks. This development becomes most pronounced on the adult living chamber. Figure 31 provides a view of the shape and proportions of cross-sections of different whorls of one of the shells, which is only moderately progressive morphologically. There exist considerably more slender as well as considerably broader shells.

The broadly rounded umbilical shoulder grades into a low and slightly convex umbilical wall. The shoulder is rather gently inclined to a shell diameter of approximately 40 mm and then again on the last whorl. The shoulder is considerably more steeply oriented and considerably less convex on the second and third before last whorls. About 70 per cent of the third before last whorl is covered by the next whorl. The relatively narrow umbilicus has a shallow appearance and is pronouncedly steplike. The living chamber occupies one whorl.

Only terminal, adult external suture lines were available for study in the BGR specimens. These were seen in kv 86 and kv 88 (Pl. 29, fig. 1A, 1B; Figures 26c, 32b), kv 277 and kv 348. The living chambers of these adult specimens begin at shell diameters ranging between 115 and 125 mm.

Judging by specimens kv 88, kv 277, kv 348 and the figured adult terminal sutures of the holotype (Koenen, 1909, Pl. XXV, figs. 1, 2), *P. clarkei* var. *stolleyi* (Koenen, 1909, Pl. XXVI, figs. 1, 2), *P. clarkei* var. *rinnei* (Koenen, 1909, Pl. XXVIII, figs. 1, 2), and specifically questionable *P. ?clarkei* var. *kokeni* (Koenen, 1909, Pl. XXVII, fig. 2), the adult external suture line of *P. clarkei* is similar to that of *Polyptychites multicostatus* Koenen 1909 in every respect, except for the presence (as a rule; see Figure 26c) of only two auxiliary lobes, only one of which is situated on the umbilical wall. However, there is at least one exception: specimen kv 88 (Pl. 29, fig. 1A, 1B; Figure 32b) appears to exhibit a narrow fifth lateral saddle subdivided by a tiny lobule and an illformed third auxiliary lobe on the innermost part of the umbilical surface. These elements resemble closely those of *P. multicostatus* (compare Figures 27, 28). Koenen (loc. cit.) figured only the ventral and lateral parts of adult suture lines but these are similar to the corresponding parts of the suture lines of the BGR specimens in every respect, including the presence of the first auxiliary lobe either on the lowermost flank or on the umbilical shoulder.

Other minor differences of the adult suture line of *P. clarkei* from that of *P. multicostatus* consist in the somewhat wider and sturdier proportions of its lobes combined with their more regular shape (compare kv 88, Figure 32b, with kv 105, Figure 28). Furthermore, the lateral and auxiliary lobes of *P. clarkei*, unlike those of *P. multicostatus*, tend to be either symmetrically or

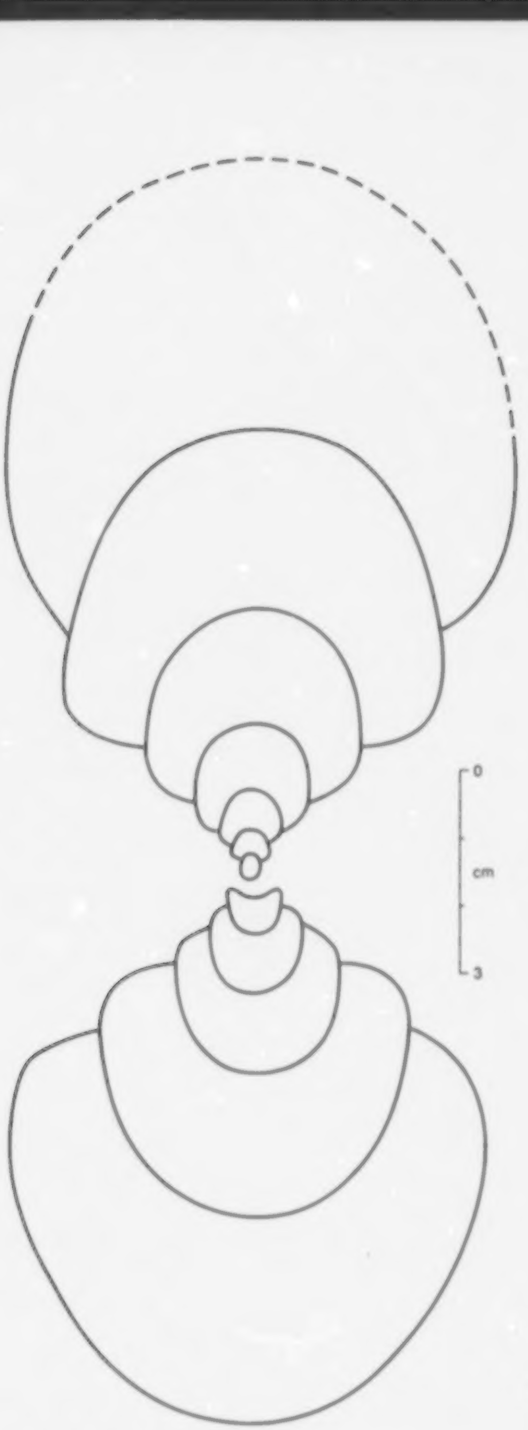


Figure 31. Cross-section of *Polyptychites clarkei* Koenen, 1909. Specimen BGR, kv 277 from Lindhorst, Northwest Germany. *Polyptychites*-Beds, upper lower Valanginian. Note the linear scale.

almost symmetrically trifid. Finally, even the adjacent terminal suture lines of *P. clarkei* (e.g. BGR, kv 88, Figure 32b; Koenen, 1909, Pl. XXVI, fig. 1) are distinctly less crowded than the advanced adult suture lines of *P. multicostatus* (e.g. BGR, kv 105; Figure 28b or BGR, kv 102). None of the studied sutures of *P. clarkei* were observed to overlap. However, there may be exceptions to the above discussed distinctions, judging by the terminal external suture line of *P. multicostatus* var. *compositus* figured by Koenen (1909, Pl. XXIII, fig. 3).

The adult external sutures of the coarsely ribbed adult specimen BGR, kv 86 appear to be abnormal (?pathologically caused) and therefore outside of the normal range of variation of adult external sutures of *P. clarkei*. In this specimen a group of five terminal external suture lines is followed by a living chamber at the whorl diameter of about 125 mm (est.). All the sutures differ from other terminal sutures lines of *P. clarkei* in the extreme shortness (and accordingly an exceptionally great width) of most of their lobes. The two lateral lobes are particularly short and wide, their length being either about equal to the width or but slightly (up to one-third) exceeding it. The ventral and the auxiliary parts of these sutures are relatively less shortened and widened. The length of the ventral lobe is, for example, between 2 and 2 1/2 times greater than its width. The length of the relatively more shortened first auxiliary lobe is about twice its width. The second auxiliary has again a greater length/width ratio while the lobule separating it from the umbilical seam is almost normally shaped and proportioned. This lobule is, therefore, almost as large as the second auxiliary and could have been mistaken for the third auxiliary lobe, except for its obvious correspondence to the proportionally smaller typical lobules of other specimens and a total absence of any lobule between it and the second auxiliary lobe.

The extreme shortening and widening of the ventral lobe and the two lateral lobes affect equally strongly their stem parts and their terminal branches. The latter have a truncated appearance and more or less rounded tips. Oddly enough, the lateral saddles of BGR, kv 86 are either not at all or only slightly narrowed in comparison with those of the normal sutures of *P. clarkei*, though their lobules are distinctly shortened and widened. All visible suture lines are strongly approximated, so that the tips of the lobes of successive lines commonly touch, and sometimes even overlap, the tops of the saddles of the preceeding lines. The lateral parts of the sutures, including the first auxiliary lobe situated on the lowermost flank, are only slightly ascendant while their auxiliary parts are subradially oriented.

A characteristic feature of the sculpture consists in an ontogenetically late transformation of primary ribs into bullae. This transformation takes place on the penultimate whorl. *P. clarkei* still has a very variable number of more or less high primary ribs (e.g. BGR, kv 86:25; BGR, kv 88:18) at whorl diameters where the ammonites of the *keyserlingi* species group have already developed typical bullae. Following the transformation of primary ribs into bullae the number of these principal sculptural elements decreases abruptly (e.g. BGR, kv 86:18/16; BGR, kv 88:16/16). The primary ribs and the bullae form a strong comma-like forward bend on the umbilical wall. They disappear approximately in the middle of the umbilical wall. During the early ontogenetic stages with shell diameters less than about 30 mm the extensions of primary ribs on the umbilical wall are radially oriented. The adult primary elements appear coarse in comparison with the predominantly fine and closely spaced primary ribs of the early whorls. This adult sculpture is reminescent therefore of that of the *keyserlingi* species group. The bullae are distantly spaced, especially on the last whorl. There they are strongly elevated and have a typical bullate shape.

The ribbing habit is known only on the adult living chamber. At the onset of the last whorl there are 5 secondary ribs per bundle. A tertiary rib occurs between the bifurcating anterior and posterior secondaries. This tertiary rib appears to be intercalated in some specimens. However, it branches off the secondary part of the anterior dichotomous element in other specimens. The bundling habit becomes more irregular on the adoral part of the adult living chamber. The number of secondaries per bundle decreases simultaneously; it is reduced sometimes to 2 secondaries per bundle. This modification occurs during a short ontogenetic stage dominated by bidichotomous bundles, which is then followed by a stage characterized by trivirgatitpartitious bundles. The above sculptural development is coupled with a weakening of ribs on the flanks.

Affinities and differences. The species resembles *P. multicostatus* in the tendency to develop relatively high and slender whorls with only feebly convex flanks and a late development of the bullae. However, *P. clarkei* differs from *P. multicostatus* in a coarse adult sculpture and broader whorls. Its adult external suture line is similar to that of *P. multicostatus*, except for possessing as a rule only two auxiliary lobes. *P. clarkei* is interpreted accordingly as a close ally of *P. multicostatus*. Its apparently more primitive adult external suture line suggests its being an independent offshoot of the ancestral stock (i.e. *P.* ex gr. *pavlowi*) of the *P. multicostatus* species group rather than a direct descendant of *P. multicostatus*. However, the infraspecific ranges of variation of these two suture lines are insufficiently well known. From the species of *P. keyserlingi* and *P. lamplughi* species groups *P. clarkei* differs first of all in a greater height of its ontogenetically advanced whorls and a relatively lesser convexity of their flanks. The adult whorls of *P. clarkei* acquire a discoidal rather than rounded cross-section. Furthermore, it differs in the ontogenetically late appearance of bullae and a much more intricately denticulated, more slender lobed adult external suture. The species cannot be confused with any other *Polyptychites* species.

P. clarkei was so far only found in Northwest Germany.

Polyptychites orbitatus Koenen 1902

Pl. 10, fig. 1; Pl. 13, fig. 4; Figures 32d, 32e.

1892 *Olcostephanus (Polyptychites) bidichotomus* Pavlow in Pavlow and Lamplugh, p. 479-480 (pars.), Pl. 16, figs. 2a-2c, 4.

•1902 *Polyptychites orbitatus* Koenen, p. 112-114, Pl. 3, figs. 1-3, 8; Pl. 4, fig. 8.

1957 *Dichotomites bidichotomus* Wright in Arkell et al., p. L348, Fig. 458, 2.

1977 *Polyptychites (Polyptychites) orbitatus* Kemper, p. 4.

Holotype. The specimen figured by Koenen (1902) in Pl. 3, figs. 1-3, 8 is the holotype of *P. orbitatus* by monotypy. These figures are not true to the original, so the holotype is refigured here (Pl. 13, figs. 4A, 4B). The original forms part of the Brandes collection and is preserved in palaeontological collections of the GIH (Catalogue of types No. 14). A plaster cast is in palaeontological collections of BGR; it is numbered as BGR, kv 278.

Locus typicus. Hoheneggelsen.

Stratum typicum. Not known precisely. However, all evidence available makes it highly probable that the holotype was collected in the basal upper Valanginian.

Material. 5 strongly deformed and fragmentary specimens including the holotype from Hollwede, Twiehausen and Hoheneggelsen. Most are from the Hollwedensis-Zone (basal upper Valanginian) at Hollwede. A supplementary, unfigured specimen is deposited in the BGR collections in Hannover under the number kv 112.

Diagnosis. Medium-sized to large species of *Polyptychites* with relatively slender whorls that are only feebly convex laterally and have a narrowly rounded venter. The relatively constant ribbing habit consists of three secondary ribs per bundle, each of which bifurcates in its turn. The adult external suture line is like that of *Polyptychites tethyale* n. sp., except in a much smaller size, slight denticulation and stubby proportions of the third auxiliary that is situated hard at the umbilical seam.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
Holotype kv 278	70	15(21)	24(34)	31(44)	29	37
kv 113	137	38(28)	41(30)	59(42)	60	74?

Description. The holotype is septate to the very end and so does not provide any information about the full size of the species. Its largest shell diameter is 86 mm. In specimen BGR, kv 279, half of the last whorl is living chamber, but is is probably not adult. In another, rather fragmentary shell the adult diameter can only be estimated. It is probably in order of 150 mm.

The width of the whorls always exceeds their height. The measured ratios of values of wh/wth amount to 24/29 and 31/37 (the holotype) for the middle growth stages. For the adult growth stage they measure 64/77 (kv 280; Pl. 10, fig. 1A). The values of whorl width are accordingly about 20 percent greater than those of the whorl's height. In spite of that the intermediate whorls appear to be relatively slender. This is because the flanks are only slightly convex and are connected by a narrowly rounded venter. Dorsalward the flanks merge into a low umbilical wall across a broadly rounded umbilical shoulder. The umbilicus is relatively narrow and shallow; it measures about 25 percent of the shell diameter. The length of the living chamber remains unknown.

No external suture lines were observed on any of the representatives of *Polyptychites orbitatus* studied in the BGR collections. The suture drawing of the smaller specimen of "*Dichotomites bidichotomous*" published by Pavlow (in Pavlow and Lamplugh, 1892, Pl. XVI, fig. 2c) and assigned to *P. orbitatus* by the writers is very incomplete. This drawing only includes the first auxiliary lobe and there is no mention of the total number of auxiliaries in Pavlow's (1892, p. 479) comments about this suture. Therefore, the morphology of the adult external suture of *P. orbitatus* is only known from two drawings of early adult sutures of its holotype published by Koenen (1902, Pl. III, fig. 8; Pl. IV, fig. 8) and reproduced here in Figures 32d and 32e. The writers were able to study a plaster cast of the holotype which only exhibits fragments of external suture lines. These appear to agree with Koenen's (l. cit.) drawings of corresponding parts of external sutures of the actual specimen but do not permit either a reconstruction of an entire suture or a count of its auxiliary lobes and saddles.

Assuming Koenen's (l. cit.) drawings to be correct, the early adult suture line of *P. orbitatus* is indistinguishable from that of *P. tethyale* n. sp. (compare Figures 32d and 32e with Figure 32c) where the shape, proportions, and complexity of all its elements but one are concerned. The only significant distinction noted consists in the actually observable (Figure 32e) or inferred (Figure 32d) positioning of the third auxiliary lobe of *P. orbitatus* suture next to the umbilical seam combined with its relatively much smaller size and but slightly denticulated, stubby appearance. The third auxiliary of *P. tethyale* n. sp. (Figure 32c) is, in contrast, a fairly large and slender, markedly denticulated structure that is separated from the umbilical seam by a wide expanse of the sixth lateral saddle including a median lobule. The external suture line of *P. orbitatus* also differs from that of *P. saxonicus* and *P. tethyale* in a more nearly symmetrically trifid arrangement of the terminal branches of its lobes. Furthermore, in the type specimen (Koenen, 1902, Pl. III, fig. 3), its adjacent sutures do not touch let alone overlap at the shell diameter of about 85 mm. In contrast, the adjacent sutures of *P. saxonicus* (including *P.* aff. *saxonicus*) not only touch but partly overlap at this and even at still earlier, growth stages (Pl. 12, figs. 1, 2A; Figures 26d, 32a). However, the unfigured specimen BGR, kv 108 of *P. saxonicus* approaches *P. orbitatus* closely in these two respects. Its lobes are almost as slender and long as those of the holotype of *P. orbitatus*. Furthermore, only some of its adjacent suture lines begin to touch and more rarely to overlap slightly at the earliest visible part of the whorl corresponding to the shell diameter of about 85 mm. The adjacent suture lines of the holotype of *P. tethyale* (Pl. 13, fig. 1A) are already touching and locally overlapping slightly at the shell diameter of about 85 mm.

From the adult external suture lines of *P. multicostatus* and *P. clarkei* that of *P. orbitatus* differs markedly in longer and more slender proportions of its subparallel-flanked lobes and in their considerably more complex and deeper denticulation. Furthermore, its saddles are relatively more narrow.

As in all members of *P. multicostatus* species group, the lateral part of the suture line of *P. orbitatus* is markedly ascendant while its auxiliary part is distinctly descendant.

The sculpture is relatively refined. Its early ontogeny is unknown. Fine bullae are present at least beginning with a whorl diameter of about 50 mm. The bullae do not become particularly prominent even in the adult growth stage where they form low elevations on the living chamber.

Three prominent secondary ribs branch from each bulla. These secondaries then subdivide in two rather high on the flank. The branching points are situated at the same level which results in a tridichotomous ribbing habit. Additional intercalated tertiary ribs occur but rarely. In the adult the ribs become lower and wider on the flanks. In such cases they are only discernible with difficulty in an oblique light. The flanks may be almost smooth in some specimens. The correspondingly reduced bullae and the secondary ribs on the adventral part of the flanks and on the venter persist right to the end of the terminal whorl. The number of secondary ribs per bundle is, as always in *Polyptychites*, somewhat reduced in the adult. Because of the disappearance of one of the tertiary branches of either the middle or the anterior secondary rib, only 4 to 5 irregularly subdividing secondary ribs remain in the bundles of the adult living chamber. These bundles do not permit any longer a differentiation of secondary and tertiary ribs.

Affinities and differences. Because of its younger and morphologically progressive adult external suture line, *P. orbitatus* must be a direct descendant of the older *P. multicostatus-P. clarkei* species subgroup that evolved out of it independently and divergently from *P. saxonicus* n. sp. and *P. tethyale* n. sp. (Figure 11). Within the *Polyptychites multicostatus* species group as a whole *P. orbitatus* resembles most closely *P. multicostatus*. The latter presumably ancestral species includes morphological variants with broader whorls, which develop quasi-tridichotomous bundling habit. *P. orbitatus* differs from *P. multicostatus* in its coarser sculpture which is more similar to that of *P. saxonicus* n. sp., in its broader whorls, more advanced, basically *P. tethyale* n. sp. -like adult external suture, and the much more slender, much more complexly denticulated and subsymmetrically trifid character of the lobes. Furthermore, its broader whorls show a stronger increase in width. Finally, *P. orbitatus* has a rather regular tridichotomous sculpture with closely adventrally situated branching points of the tertiary ribs. This sculpture is present at least on the three outermost whorls of its phragmocone.

P. saxonicus has a shell shape similar to that of *P. orbitatus*. However, its ribbing habit is not tridichotomous because of the presence of additional tertiary ribs. Finally, the bundling habit of *P. saxonicus* is characterized by more addorsally situated branching points and a considerably more irregular arrangement of secondary and tertiary ribs which reminds one of the heteroptychous arrangement of ribs in some *Prodichotomites* species.

Although *P. orbitatus* shares the regularly tridichotomous bundling habit with *P. hapkei*, its sculpture is considerably more refined and more closely spaced. The two species differ also in the shape of the shell, as the whorl of *P. hapkei* n. sp. is considerably wider in the intermediate growth stages, and the morphology of the suture line. As already mentioned, the sculptural similarity of these two species appears to be a matter of homoeomorphy only.

The species occurs in Northwest Germany and eastern England (Speeton).

Polyptychites saxonicus n. sp.

Pl. 11, fig. 3; Pl. 12, figs. 1, 2, 4; Pl. 13, fig. 3;
Figures 26d, 32a.

Derivation of name. From the occurrence in Lower Saxony.

Holotype. The original of Pl. 12, figs. 2A, B, which is preserved in the GIH, Cat. No. 2517. Plaster cast numbered kv 109 is preserved in the BGR collections, Hannover.

Locus typicus. Hoheneggelsen.

Stratum typicum. Though this is not known precisely, all available evidence suggests that the species occurs in the basal upper Valanginian, presumably in the upper Hollwedensis-Zone.

Material. 8 poorly preserved specimens from Hoheneggelsen, Hollwede and Twiehausen. These specimens have been found in the Lower/Upper Valanginian boundary beds and in the basal upper Valanginian.

Diagnosis. A large species, the whorls of which have only feebly convex flanks with narrowly arched venter. The whorls are moderately broad to broad. The sculpture is fine and dense and with an irregular subdivision of primaries. The secondary ribs are of an unequal strength. Tertiary ribs are numerous; there are 6 to 9 per bundle in the intermediate growth stages. The adult external suture line has three well developed auxiliary lobes and approaches that of *P. tethyale* n. sp. in the complexity and depth of denticulation of its elements.

Measurements (in mm).

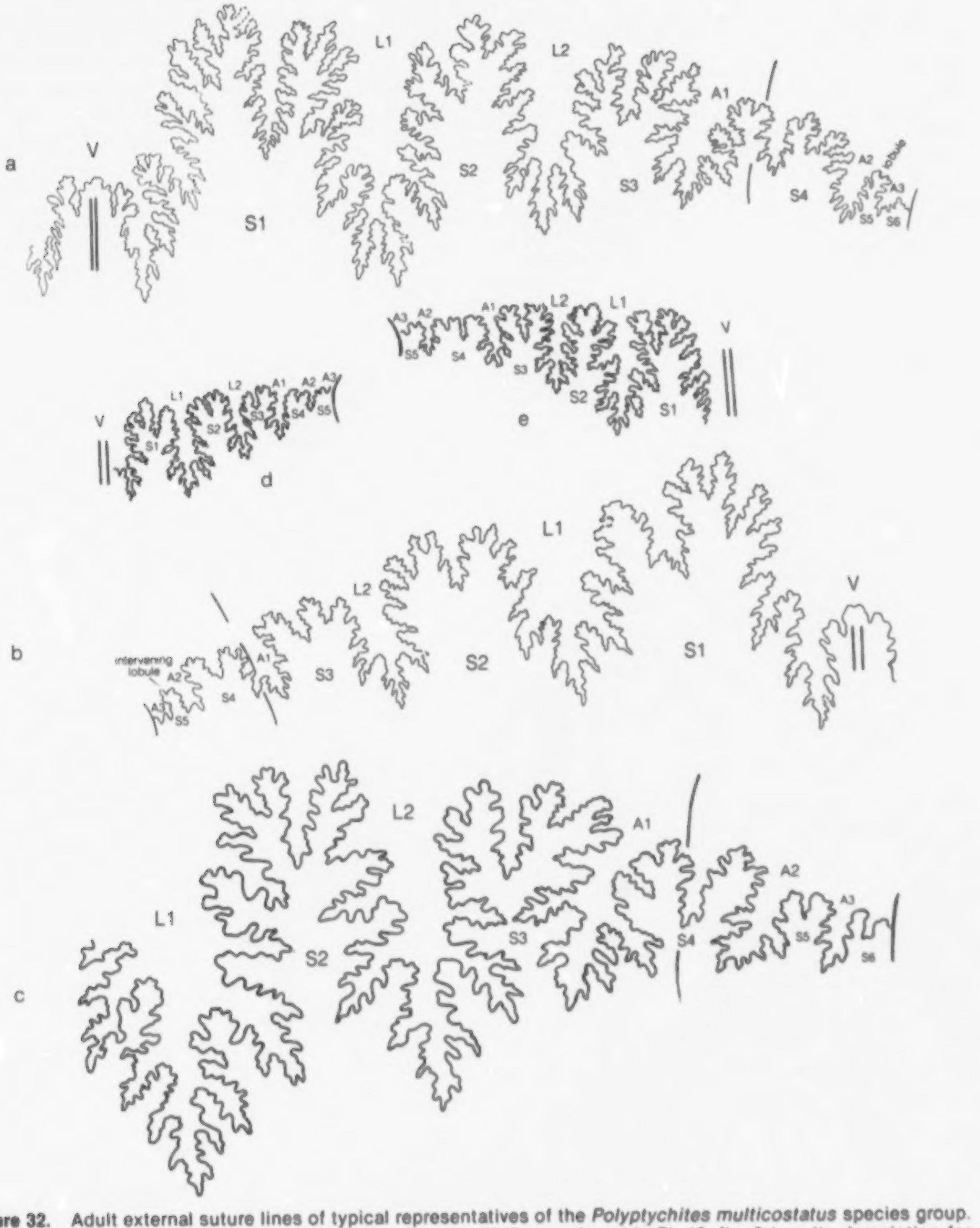
Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
Holotype kv 109	101	24(24)	33(33)	45(45)	—	50?
kv 281	131	39(30)	39(30)	54(41)	57	77
kv 114	165	46(28)	53(32)	66(40)	66	82
kv 110 (aff.)	105	25(24)	36(34)	45(43)	34?	46?

Description. The holotype is septate to the end, so that its adult size remains unknown. It affords a view of the appearance of the intermediate growth stages. Only the last whorl of all other specimens (except for kv 110) was available for study. According to these specimens, the adult size of the species is approximately 170 mm.

The greatest width of the whorl is situated at the level of the umbilical shoulder. It is, as a rule, considerably greater than the height of the whorl and increases moderately in the course of the ontogeny. The rate of increase of whorl width commonly increases considerably in the adult (e.g. kv 281). The flanks are only slightly convex while converging rapidly adventrally. The venter is correspondingly narrowly rounded. The umbilical shoulder is broadly rounded. The umbilical wall is steeply oriented in the intermediate growth stages but becomes more gently inclined in the adult, where it may become convex. The umbilicus is relatively narrow (24 to 30 percent) and, except in the adult, rather shallow. The succeeding whorls enclose 74 percent of the preceding whorls in the holotype where the umbilicus is step-like. The living chamber occupies at least one whorl.

The external suture line of *P. saxonicus* (including the aberrant specimen kv 110 designated as *P.* aff. *saxonicus* n. sp.; Pl. 12, fig. 1, Pl. 13, fig. 3; Figure 26d) was studied in the specimens kv 108, 109, (Pl. 12, fig. 2; Figure 32a), 110 and 111 at shell diameters ranging from 73 to 110 mm. In spite of the fact that the specimens concerned are septate to the end, all of these sutures appear to be advanced rather than early adult sutures because of their strong crowding and partial overlap. The adult living chambers of some other representatives of *P. saxonicus* (e.g. kv 114; Pl. 11, fig. 3) begin at a shell diameter of 170 mm. The reason for this apparent discrepancy is not known. All of the suture lines studied are of the same type regardless of the shell diameter.

The external suture line of *P. saxonicus* differs from that of *P. multicostatus* first of all in a relatively greater slenderness and length of all its elements combined with a greater crowding of adjacent suture lines (Pl. 12, fig. 2B; Figures 26d, 32a). The lobes and saddles of adjacent suture lines begin to touch and even to overlap in places already on the innermost whorls studied (e.g. at a shell diameter of about 72 mm; Pl. 12, fig. 2B) when the adjacent sutures of *P. multicostatus* are, as a rule, still either narrowly separated or just touch each other in places.


a
V
L1
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A1
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lobule
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S6
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d
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intervening lobule
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S2
S1
S4
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A3
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S3
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c

Figure 32. Adult external suture lines of typical representatives of the *Polyptychites multicostatus* species group. **a**. *P. saxonicus* n. sp. Holotype, GIH collections, Cat. No. 2517 reproduced in Pl. 12, fig. 2 (see its description for further details). Advanced? adult suture observed at the whorl height of about 50 mm, x 3. **b**. *P. clarkei* Koenen, 1909. BGR, kv 88 reproduced in Pl. 29, fig. 1 (see its description for further details). Combination of two oralmost sutures before adult living chamber at the whorl height of 44 mm, x 3 (approx.). **c**. *P. tethyale* n. sp. Holotype, BGR kv 282 reproduced in Pl. 13, fig. 1 (see its description for further details). Incomplete (no ventral lobe) advanced? adult suture observed at the last preserved whorl of this wholly septate specimen at the whorl height (wh) of about 42 mm, x 4 (approx.). **d,e**. P. *orbitatus* Koenen, 1902. Holotype, GIH collections, Cat. No. 14. Hoheneggelsen, Northwest Germany. Probably from basal upper Valanginian, upper Hollwedensis Zone. Reproduction of two early adult sutures drawn by Koenen, 1902, Pl. III, fig. 8 (Fig. 32d) and Pl. IV, fig. 8 (Fig. 32e), x 1.

Another important distinction is a much more complex and deep denticulation of all elements of the suture line of *P. saxonicus* as compared with their equivalents in the *P. multicostatus* suture line. In combination with the crowding of adjacent sutures, this complex and deep denticulation produces an extremely fine, intricate and closely interwoven sutural pattern on the flanks and venter of *P. saxonicus*. Among the presently known NW European *Polyptychites* species the intricacy of this pattern is matched only by that of *P. tethyale* (Pl. 13, figs. 1A, B; Figure 32c) and *P. orbitatus* (Figures 32d, 32e). Because of this relative lengthening and attenuation of all lobes in *P. saxonicus*, all its saddles, except for the fifth lateral saddle of typical representatives (see below), have become considerably wider than those of *P. multicostatus*. All of them, including the first lateral saddle (Pl. 12, fig. 2A; Figure 26d), are appreciably to much (especially the fourth lateral saddle) wider than the preceding lobes.

The increase in complexity of the *P. saxonicus* suture line in comparison with that of *P. multicostatus* is most pronounced in the second auxiliary lobes and adjacent lobules of the fifth lateral saddles (Figures 26d, 32a). The second auxiliary lobe of *P. saxonicus* is considerably larger and more strongly constricted at the top. At the same time, it is considerably more strongly expanded and much more complexly and deeply denticulated in the lower part where its secondarily notched terminal branches have almost lost the asymmetrically trifid arrangement characteristic of *P. multicostatus* branches (compare Figure 32a). The previously described barely noticeable to small, simple lobule subdividing the top of the fifth auxiliary saddle in *P. multicostatus* (Figures 27, 28) retains that appearance in most of the studied representatives of *P. saxonicus*. In these specimens the fifth lateral saddle retains the extremely small width (e.g. Figure 32a) characteristic of *P. multicostatus*. However, this lobule is transformed into a much larger, sturdy (only slightly longer than wide) asymmetrically bifid and fairly deeply notched structure in some other specimens, which are designated *P. aff. saxonicus*. In these morphologically and presumably evolutionarily advanced specimens (e.g. in kv 110; Pl. 12, fig. 1; Pl. 13, fig. 3; Figure 26d), the enlargement of this lobule is combined with a strong widening of the fifth lateral saddle. This saddle becomes about twice as wide as the preceding second auxiliary lobe and occupies most of the outer half of the umbilical wall.

In most of the sutures studied the third auxiliary lobe is a sturdy (only a slightly longer than wide), asymmetrically trifid to irregularly shaped, fairly deeply denticulated structure that occurs within the inner quarter of the umbilical wall but is always separated from it by a partially exposed sixth lateral saddle (e.g. Figure 32a). In these typical specimens this auxiliary is usually only half as long but almost to quite as wide as the second auxiliary lobe. It is relatively larger and more complexly denticulated than the third auxiliary lobe of *P. multicostatus*. As in *P. multicostatus*, the nature of this third auxiliary is indicated by the presence of a small and simple, tack-like shaped lobule in the preceding fifth lateral saddle.

Unlike the third auxiliary lobe of *P. multicostatus* that is always situated either next to or in the close proximity of the umbilical seam, the third auxiliary of these typical representatives of *P. saxonicus* is separated from the umbilical seam by the partly (?largely) exposed sixth lateral saddle, the visible width of which is subequal to that of this auxiliary (Figure 32a).

The third auxiliary lobe of the aberrant specimen of *P.* aff. *saxonicus* is positioned still farther away from the umbilical seam, approximately between the middle and inner thirds of the umbilical wall (Figure 26d). This lobe is considerably more slender and long (being 1 1/2 to 2 times longer than wide) than the typical third auxiliary lobe. Furthermore, it is much more regularly shaped (adapically tapering to parallel-flanked), regularly trifid, and relatively larger than the other variant. In all these features the third auxiliary of *P.* aff. *saxonicus* resembles closely that of *P. tethyale* (compare Figure 32c).

The presumably largely exposed sixth lateral saddle of *P.* aff. *saxonicus* (Figure 26d) occupies the inner third of the umbilical wall. It is approximately flat topped and is subdivided into two subequal parts by a small, simple or slightly serrated, tack-like lobule that is flanked by tiny notches on both sides. This saddle is similar to that of *P. tethyale* n. sp., except that its median lobule is relatively much smaller. No part of the fourth auxiliary lobe is exposed in any of the sutures studied.

The sculpture of *P. saxonicus* n. sp. is dense and refined in terms of relationships characteristic of the genus. Its early ontogeny is unknown. 16 primary elements per whorl occur in the holotype at a shell diameter of 55 mm. At first these are approximately radially oriented primary ribs. Later these ribs rapidly acquire a bullate appearance, especially because of the strong forward bends of their extensions on the umbilical wall. At a shell diameter of 80 mm this bend of the extensions of the bullae is more strongly expressed than in any other species of Polyptychitinae. However, the bend decreases again in the adult. The bullae are feebly developed and low in all growth stages, including the adult one. The number of bullae per whorl comprises about 16 in the presumably adult shells (kv 114; Pl. 11, fig. 3 or kv 281).

The ornament is particularly dense and fine in the holotype. No bundling is discernible until a shell diameter of 70 mm because of poor preservation. The next stages permit a clear differentiation of secondary and tertiary ribs. On the average the bullae subdivide into three secondary ribs, to which are subordinated from 5 to 8 tertiary ribs. The secondary ribs commonly are of an unequal strength. Furthermore, some of them are simply intercalated instead of being connected with the bullae. Only some of the tertiary ribs arise either through dichotomous subdivision or splitting off. Their starting points are situated on the adventral halves of the flanks at a variable height (commonly rather adventrally). The ribbing habit must, therefore, be designated as irregular. The same is true of the adult growth stage (kv 114; Pl. 11, fig. 3 or kv 281) where the number of secondary ribs per bulla is, as always, reduced. The number of tertiary ribs decreases in this growth stage to 4-6.

Two unfigured specimens are preserved in the palaeontological collection of BGR in Hannover as nos. kv 198 and kv 111.

Affinities and differences. Because of the morphology of its shell habitus, sculpture and adult external suture line combined with an appreciably younger age, *P. saxonicus* belongs to that finely and closely ribbed late *Polyptychites orbitatus* subgroup which arose out of the *P. multicostatus* subgroup. It appears to be a direct descendant of *P. multicostatus* (Figure 11). As already pointed out in the description of *P. multicostatus*, this older species is particularly close to *P. saxonicus* in most aspects of its morphology. The differences from *P. multicostatus* consist in a larger-sized and wider shell, in very adventrally situated starting points of the tertiary ribs and in a much more complexly denticulated, slender lobed and more crowded suture line with a better developed third auxiliary lobe and partly exposed sixth lateral saddle. The sculpture of *P. saxonicus* is more closely spaced and finer than that of the contemporary *P. orbitatus*. *P. saxonicus* is also distinguished from *P. orbitatus* by its very irregular bundling with a higher number of tertiary ribs per bundle.

The distinctions from *P. tethyale* are described under that species. The whorls of *P. saxonicus* are more narrow and its venter more narrowly arched in comparison with those of the contemporary *P. hapkei*. Furthermore, its sculpture is considerably more dense and more refined and is characterized by very irregular bundling. Finally, the extremely complexly denticulated, slender lobed and crowded external suture line of *P. saxonicus* differs sharply from much more simple, relatively more broadly and widely lobed and considerably more widely spaced suture of *P. hapkei* n. sp. Judging by their morphology, neither *P. hapkei* nor the ancestral *P.* ex gr. *keyserlingi* are directly genetically related to *P. saxonicus*. The species is so far only known from Northwest Germany.

Polyptychites tethyale n. sp.

Pl. 13, figs. 1A, 1B, Figure 32c.

1977 *Polyptychites* aff. *plicatilis* (of Koenen 1902) Thieuloy, p. 412, 413, Pl. 7, fig. 1.

Derivation of name. From the original description of the species in the Tethyan Realm (Southeast France).

Holotype. The original of Pl. 13, figs. 1A, 1B. Preserved in the BGR collections, kv 282.

Locus typicus. Twiehausen.

Stratum typicum. Basal upper Valanginian, Hollwedensis-Zone.

Material. Two specimens, 1 from Northwest Germany (Twiehausen) and one from Southeast France (Le Bourguet).

Diagnosis. A medium-sized species with relatively low and almost tubular whorls. The sculpture is fine and very dense with a quasi-tridichotomous bundling habit. The adult external suture line is essentially like that of *Polyptychites saxonicus* and *P. orbitatus*, except that the large third auxiliary lobe is slender and followed by the almost fully exposed, wide sixth lateral saddle.

Description. The holotype is deformed and so does not afford any reliable measurements. It would be insufficient for erection of a new species, except for the availability of a second, relatively well preserved specimen from Southeast France (Thieuloy, 1977, Pl. 7, fig. 1).

The holotype (maximum diameter about 110 mm) is septate to the end. The size of the adult shell remains unknown. However, it seems likely that the shell reached a medium size for the genus. The oralmost part of the last whorl appears to be the least deformed. If its appearance is not deceptive, the greatest width of the whorl is situated not at the level of the umbilical shoulder but nearer the venter. Therefore, the relatively low whorls have a tubular appearance. The umbilical shoulder is broadly rounded and merges gradually into a relatively gently inclined umbilical wall. The moderately broad umbilicus is funnel-like, as the successive whorls almost completely enclose the preceding whorls.

The advanced adult external suture line, which is clearly visible on the holotype (Pl. 13, figs. 1A, 1B; Figure 32c), is of the same general type as that of *P. saxonicus* and *P. orbitatus* (see there for further details). It is much more complex and morphologically more advanced than that of any other representative of the *Polyptychites multicostatus* species group. The suture line of *P. tethyale* is strongly ascendant in its lateral part and distinctly descendant in its auxiliary part like those of all other representatives of this species group.

The observed differences from the adult external suture line of *P. saxonicus* (including *P.* aff. *saxonicus*) consist in:

1. A distinctly lesser width of the first to fourth lateral saddles, which are either about as wide as or only slightly wider than the preceding lobes. The second and third lateral saddles are particularly narrow. They are all but crossed by the largest lateral branches of their flanking lobes, which almost meet in the middle (Figure 32c). The fifth and sixth lateral saddles are, in contrast, widened in comparison with the equivalent saddles of *P. saxonicus* (see p. 78 for further details). All lobes and lobules are more complexly and more deeply denticulated than their equivalents in *P. saxonicus*.
2. Symmetrically to almost symmetrically trifid arrangement of terminal branches of the two lateral lobes and the first auxiliary lobe; and
3. Considerably more slender proportions and greater crowding of auxiliary lobes, including the third auxiliary. The latter is followed by almost completely exposed, uniquely wide sixth lateral saddle.

The absence of comparative material of *P. tethyale* makes it impossible to say whether or not the above distinctions are constant features suitable for the differentiation of these two species.

The distinction of *P. tethyale* suture from that of *P. orbitatus* were discussed in the description of the latter.

The sculpture is very fine and dense. The last preserved whorl has 20 refined bullae. Their extensions on the umbilical wall are strongly bent forward, which results in a comma-like appearance of the bullae. At least 3 secondary ribs branch from each bulla. At first these secondaries subdivide into two branches on the mid-flank. However, this subdivision point moves higher and higher upflank on the oral half of the last preserved whorl. The sculpture become more irregular on this half of the whorl because of the appearance of additional intercalated secondaries and also because of an unequal strength of the secondary ribs. This sculpture agrees rather well with that of the specimen figured by Thieuloy (1977, Pl. 7, fig. 1).

Affinities and differences. *P. tethyale* belongs to those very distinctive, late *Polyptychites* ex gr. *orbitatus* which are characterized by a fine and very dense sculpture. It is most closely allied to *P. saxonicus* from which it differs in a wider umbilicus, a low, tube-like whorl shape and the already discussed morphological details of its suture line. Furthermore, it has a smaller number of tertiary ribs per bundle than does *P. saxonicus*.

The species was so far only found in Northwest Germany and Southeast France.

Polyptychites sublatissimus Spath 1924

1906 *Olcostephanus (Polyptychites)* cf. *Keyserlingi* Danford, Pl. 10, figs. 3, 3a.

*1924 *Polyptychites sublatissimus* (= cf. *Keyserlingi* of Danford, 1906) Spath, p. 75.

Discussion. The solitary holotype of *P. sublatissimus* Spath 1924 (Danford, 1906, Pl. 10, figs. 3, 3a) is so poorly preserved that the erection of a new species for this specimen by Spath (1924, p. 75) was not justified. The species remains questionable and its status uncertain. It is only possible to say that *P. sublatissimus* has broad whorls and belongs to the closely and finely ribbed late *Polyptychites* forms. It is indubitably closely related to *P. tethyale*.

Polyptychites sphaeroidalis Koenen 1909

*1909 *Polyptychites sphaeroidalis* Koenen, p. 20-22, Pls. 5, 6.

1909 *Polyptychites conglobatus* Koenen, p. 22, Pls. 7, 8.

Holotype. The specimen figured by Koenen (1909, Pls. 5, 6) is the holotype of *P. sphaeroidalis* by monotypy. It is preserved in the collections of the Geological Institute, Goettingen.

Material. Two specimens described and figured by Koenen (1909) and listed above in the synonymy.

Locus typicus. Lindhorst.

Stratum typicum. Upper *Polyptychites*-Beds (= upper lower Valanginian).

Description. Neither of the two representatives of *P. sphaeroidalis* described and figured by Koenen (1. cit.) was re-studied by the writers. Therefore, they cannot add anything to its description, except for a few comments on the external suture line.

The incomplete adult external suture lines are visible on the holotype of *P. sphaeroidalis* (Koenen, 1909, Pls. V, VI) and on that of "*P. conglobatus*" that is here synonymized with the former species. The visible (painted white) parts of these terminal suture lines are similar in all significant details and so will be described summarily. They are morphologically similar to the "conservative" external sutures of *P. keyserlingi* (e.g. Figures 25b, 25d) in the shape, proportions, denticulation and localization of their elements. As in *P. keyserlingi*, only two lateral lobes and all of the very wide and complexly denticulated third lateral saddle are situated on the flanks of *P. sphaeroidalis*. The first auxiliary lobe, which is only visible in "*P. conglobatus*" (Koenen, 1909, Pl. VIII), is situated entirely on the outer part of the umbilical wall. The only faintly visible second (and last) auxiliary lobe, which is also only visible in "*P. conglobatus*", appears to be situated either at or close to the umbilical seam.

The suture line of the holotype appears to be only slightly ascendant on the flank. That of "*P. conglobatus*" is markedly (some 15 to 20 degrees, est.) and approximately evenly ascendant on the flank. Then it appears to become somewhat suspensive on the outer part of the umbilical wall at least.

Discussion. As interpreted here, the species of *P. sphaeroidalis* is based on two adult living chambers. Therefore, it is only possible to say that this species is larger than *P. keyserlingi* and differs from this similarly proportioned species in a strong weakening of the ornament on the adult living chamber. Because of the absence of early and intermediate growth stages, it is not possible to make any observations about the ontogenetic development of the species. As the knowledge of the morphology of the early and intermediate growth stages is decisive for the interpretation of the younger representatives of *Polyptychites*, a definitive evaluation of *P. sphaeroidalis* is impossible. Nevertheless, the morphology of its terminal external suture line and its stratigraphic position suggest its being a connecting link between *P.* ex gr. *keyserlingi* and *P. hapkei* n. sp. What little is known otherwise of its adult morphology is compatible with this suggestion.

Despite the poor knowledge of *P. sphaeroidalis*, the broad-whorled, late early and early late Valanginian Polyptychitinae with a tridichotomous sculpture were previously assigned to it (Kemper, 1975, 1976, 1977; Kemper, Ernst and Thiermann, 1978). Furthermore, the name *sphaeroidalis* was used by these workers as an index of the latest early to early late Valanginian paleontological zone where these tridichotomous forms with narrow juvenile shells occur. This usage is abandoned herein and these younger *Polyptychites* forms are described below as a new species *P. hapkei*.

Polyptychites hapkei n. sp.

Pl. 9, figs. 3, 4; Pl. 10, fig. 3; Pl. 11, fig. 1; Pl. 13, fig. 2; Pl. 28, fig. 2; Figures 33a, 33b, 36b

1892 *Olcostephanus (Polyptychites) bidichotomus* Pavlow (in Pavlow and Lamplugh), p. 479, 480 (pars), Pl. 16, figs. 3a, 3b.

?1929 *Polyptychites* sp. aff. *ovatus* Frebold, p. 11, 12; Pl. 4, fig. 3.

?1929 *Polyptychites* sp. aff. *Tscherskii* Frebold, p. 12; Pl. 6, fig. 3.

1937 *Polyptychites sphaeroidalis* Stolley, p. 447.

1951 *Bidichotomites bidichotomus* Sazonov, p. 57-59, Pl. 1, fig. 1.

1975 *Polyptychites sphaeroidalis* Kemper, p. 248, 249.

1976 *Polyptychites sphaeroidalis* Kemper, p. 38.

1977 *Polyptychites sphaeroidalis* Kemper, p. 4, 5.

1978 *Polyptychites sphaeroidalis* Kemper, Ernst and Thiermann, p. A1-11, A1-17.

Origin of name. For Mr. Wilhelm Hapke in recognition of his outstanding collecting activities, especially at Hollwede.

Holotype. The original of Plate 10, fig. 3; Pl. 28, fig. 2; Figure 33a of this paper preserved in the collections of the BGR in Hannover, Type Cat. kv 285.

Locus typicus. Hollwede.

Stratum typicum. Topmost lower? and basal upper Valanginian.

Material. 16 specimens from Hollwede and Twiehausen.

Diagnosis. Medium-sized to large species with a low and broad whorl section in the intermediate and adult growth stages. Juvenile whorls to a shell diameter of about 60 mm relatively narrow. Ornament is coarse and regular. Three bifurcating secondary ribs branch from each bulla, at least in the intermediate growth stages. The adult external suture is similar to that of *P. keyserlingi* except that its most progressive examples may become *Polyptychites saxonicus*-like and/or acquire the fourth auxiliary lobe.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh l	wh 2	wth 1	wth 2
BGR, kv 385 Holotype	127	40(31)	40(31)	47(37)	65	76
BGR, kv 89	146	43(29)	40(27)	63(43)	71	86?
BGR, kv 286	120	39(32)	34(28)	47(39)	61	73
BGR, kv 92	82	25(30)	25(30)	32(39)	38?	48?
BGR, kv 284 (juv.)	48	13(27)	20(42)	15(31)	19?	25?
BGR, kv 279	108	29(27)	36(33)	43(40)	60?	—

Description. Almost the whole of the last whorl of the holotype is occupied by the living chamber. It exhibits senile features, such as the irregularity of ribbing habit, at the end. This indicates that this specimen is an adult with a terminal shell diameter of about 140 mm. It belongs to the smaller representatives of the species. The umbilicus is moderately wide and step-like rather than funnel-like. The shell is relatively strongly involute. The holotype exhibits only the morphology of the last whorl, which is broadly arched and considerably wider than high. The slightly convex umbilical wall is steep at the beginning of the last whorl and then becomes increasingly more gently inclined to the end of the whorl.

Because the holotype exhibits the adult growth stage, its sculpture does not exhibit any more the most characteristic tridichotomous rib bundles, which are essentially restricted to the intermediate growth stages. Only one such bundle is still present at the end of the earliest quarter of the whorl. All others exhibit signs of dissolution. They either lack one of the tertiary ribs or have only two bifurcating ribs that are connected with the same bulla. Furthermore, their subdivision point migrates toward the dorsum. No definite bundling pattern is recognizable anymore on the oral half of the last whorl.

The size of the species fluctuates between 130 and 200 mm. It exhibits a great variability, especially where the rate of increase of the whorl's width is concerned.

One specimen (BGR, kv 284; Pl. 9; figs. 4A-4C; Pl. 13, fig. 2) permits an insight into the ontogeny of the whorl shape. The whorls are relatively slender and high until a shell diameter of about 60 mm. Then they rapidly become broad and low. In this *Euryptychites*-like growth stage (Pl. 9, fig. 4C), the venter is a wide, regular arch. The whorl shape changes considerably in the more advanced growth stages. There the only feebly convex, rapidly adventrally converging flanks merge in a relatively narrowly rounded ventral region. The relationships observed in this shell may be considered as moderately progressive. The more progressive variants remain more *Euryptychites*-like into the adult growth stage where they retain low and more or less evenly arched whorl cross-sections.

The umbilical shoulder is rounded in all growth stages. However, this rounding is least marked on the *Euryptychites*-like whorls of the intermediate growth stages. The umbilical wall is relatively low; it is only moderately steeply oriented and slightly convex. The width of the umbilicus comprises approximately 30 percent. The living chamber is at least one whorl long.

The following evaluation of the adult external suture line is based on the study of BGR specimens kv 279, kv 284, kv 285 (the holotype), kv 286, kv 344, and drawings of the large representative of "*Olcostephanus (Polyptychites) bidichotomus*" of Pavlow (in Pavlow & Lamplugh, 1892, Pl. XVI, figs. 3a, 3b), which is synonymized with *P. hapkei* by the writers. In spite of a smaller number of examples available, this suture was found to be even more variable morphologically than that of *P. keyserlingi*, which it much resembles in most aspects.

One morphological extreme is typified by the BGR, kv 344 (Figure 36b), BGR, kv 285 (the holotype; Figure 33a), and the specimen figured by Pavlow (1. cit.). It is designated the **conservative variant** because of the characteristic presence of only two auxiliary lobes. All other morphological details of this variant are rather variable. The terminal suture of BGR, kv 344 (Figure 33a) is the most complexly and deeply denticulated example known. Its uniquely wide and sturdy lobes are constricted at the top, instead of tapering apicalward. The lobules are exceptionally thick and commonly roundtipped. The first and second lateral saddles are correspondingly narrowed. The first saddle is about as wide as the ventral lobe while the second is considerably more narrow than the first lateral lobe. However, the third and fourth lateral saddles are uniquely wide, in spite of an exceptional width and complexity of their preceeding lobes. The third saddle is three times wider than the second lateral lobe. This flat-topped, richly and deeply denticulated saddle occupies most of the inner third of the flank, all of the umbilical shoulder, and the outermost part of the umbilical wall (Figure 36b).

The exceptionally large, complexly denticulated, and asymmetrically trifid first auxiliary lobe occupies most of the outer third of the umbilical wall. The following fourth lateral saddle, is halved by an exceptionally large, slender but only simply denticulated lobule.

The size of unusually large second and last auxiliary lobe is about one half that of the first auxiliary. This slender, fairly deeply denticulated, asymmetrically trifid lobe is separated from the umbilical seam by the greater outer part of the fifth lateral saddle which is somewhat wider than the auxiliary. A slender, parallel-sided, simply notched lobule partly visible at the umbilical seam is also uniquely large; it is almost as long as the second auxiliary.

The advanced adult external suture of *"Olcostephanus (Polyptychites) bidichotomus"* Pavlow (in Pavlow & Lamplugh, 1892, Pl. XVI, figs. 3a, 3b) is comparably slender and long to and similarly richly and deeply denticulated as that of BGR, kv 344 (Figure 36b). However, all its lateral saddles, including the fourth, are narrow and less complexly denticulated. The very large second auxiliary is situated hard at the umbilical seam.

The external sutures of the holotype (BGR, kv 285; Pl. 10, fig. 3; Figure 33a), which immediately precede its adult living chamber at the shell diameter of about 120 mm, are the other morphological extreme in the conservative variant. All their lobes are relatively more narrow but adapically tapering, more sparcely and shallowly denticulated than those of BGR, kv 344. The first auxiliary lobe of kv 285 sits on the innermost part of the flank while the second auxiliary is situated in the middle of the umbilical wall (Figure 33a). The first and second lateral saddles differ in being appreciably (the first) to much (the second) wider than the preceding lobes. The remaining third to fifth lateral saddles are subequally wide and, at the same time, considerably wider than the preceding lobes. The third lateral saddle of the holotype is not widened at all, in contrast with BGR, kv 344 (compare Figures 33a and 36b) and all its saddles are relatively more sparcely and more shallowly denticulated. The very sturdy and short, broadly triangular lobule of the fifth lateral saddle is larger than the median lobule of the fourth saddle. This abnormally large, oddly shaped lobule may be pathologically malformed.

Only the two lateral lobes of the holotype are markedly ascendant (at 10 to 15 degrees). The third lateral saddle and the rest of the suture are distinctly descendant. All three sutures are closely spaced with the tips of the lobes commonly approaching closely the tops of the saddles of preceding lines. However, these elements do not touch anywhere.

In *P. keyserlingi*, the adult external sutures of BGR, kv 338 and *P. k.* var. *tschernyscheffi* (Koenen, 1909, Pl. XIV, figs. 2, 3) resemble closely that of BGR, kv 344. The suture of BGR, kv 338 (Figure 25b) almost duplicates the latter, except for a relatively more narrow and differently denticulated third lateral saddle which is similar to that of *"Olcostephanus (Polyptychites) bidichotomus"* Pavlow (1. cit.). The suture lines of the specimen of *P. keyserlingi* reproduced in Figure 25d and its specimen BGR, kv 338 (Figure 25b) resemble closely the terminal sutures of the holotype of *P. hapkei*, except for the more sparse and shallow denticulation of the latter and the positioning of its first auxiliary lobe. The ventral and lateral parts of the holotype's sutures are also similar to those of *P. keyserlingi* var. *infundibilum* Koenen (1909, Pl. III, figs. 1, 2) and *P. k.* var. *robustus* Koenen (1909, Pl. III, figs. 3, 4). The terminal external suture lines of *P. sphaeroidalis* Koenen (1909, Pls. V-VIII) are also similar to those of the holotype of *P. hapkei*, except that the shape and denticulation of their lobes and saddles resemble more closely those of the specimen BGR, kv 344. The conservative suture line of *P. hapkei* merges imperceptibly into the conservative variant of the *P. keyserlingi* suture and into the similar suture of *P. sphaeroidalis*. These three sutures cannot be reliably distinguished.

The other extreme variant of adult external suture of *P. hapkei* is characterized by the presence of three, and occasionally four, auxiliary lobes. This progressive variant is typified by the early to advanced adult sutures of specimens BGR, kv 286 (Figure 36c), kv 284 (Figure 33b) and kv 279 (unfigured).

Except for the increased number of auxiliaries, the morphology of the progressive sutural variant is even more variable than that of the conservative variant. The early adult sutures of BGR, kv 286 (Figure 36c) examplify one morphological extreme. These sutures, which possess three auxiliaries, are characterized by a degree of complexity and depth of denticulation of all their elements that is unique for *P. hapkei*. This extreme denticulation is combined with an equally extreme slenderness of all lobes and a unique narrowing of both lateral saddles. In all these features, the sutures of BGR, kv 286 are only comparable with those of the *Polyptychites multicostatus* species group, particularly with those of *P. saxonicus* (compare Figure 36c with Figures 26d and

32a). However, this similarity appears to be a matter of homoeomorphy for reasons presented in the description of *P. multicostatus* species group.

The ventral lobe of BGR, kv 286 is about three times longer than wide and distinctly longer than the first lateral lobe. The latter is about 3.5 times longer than wide, subparallel-flanked, slender-stemmed, and asymmetrically trifid. The first and second lateral saddles are strongly narrowed and about as wide as the preceding lobes. The above mentioned lobes and saddles are deeply dissected by long and slender, acutely pointed lobules, the principal branches of which are denticulated in turn. The principal flanking lobules of the ventral and first lateral lobes almost meet in the middle of the first lateral saddle.

The second lateral lobe, which occupies the flank's middle, is parallel-flanked and symmetrically trifid; it is distinctly sturdier (about 2.5 times longer than wide) than the first lateral lobe and its length is about three-quarters that of the latter. The denticulation of the second lateral lobe is similar to that of the first, except that its principal lobules are shorter, somewhat less complexly dissected, and do not penetrate as deep into the second lateral saddle as do those of the first lateral. The following, trapeze-shaped third lateral saddle is up to 2 times wider than the second lateral lobe. This saddle is as deeply and complexly denticulated as the preceding saddle; it is restricted to the inner, but not the innermost, part of the flank.

The first auxiliary lobe situated entirely on the lowermost flank is adventrally inclined at 30 to 40 degrees. This symmetrically trifid, moderately deeply and complexly denticulated, slender-stemmed lobe is about 3.5 times longer than wide.

The flattopped, fourth lateral saddle spans the innermost flank, the umbilical shoulder, and the outermost umbilical wall. It is moderately richly denticulated and about three times wider than the preceding lobe.

The long and slender (up to 3 times longer than wide) second auxiliary lobe occupies the middle of the umbilical wall; it is a pronouncedly asymmetrically trifid but otherwise only simply and shallowly denticulated structure that is about half as large as the first auxiliary lobe. The following, irregularly shaped fifth lateral saddle is about two times wider than this lobe; it bears a small and simple, submedian lobule.

The third auxiliary lobe is a long and slender (up to 2 1/2 times longer than wide), acutepointed and but slightly notched structure with subparallel flanks. Its length is about two-thirds that of the second auxiliary but it is only slightly more narrow than the latter. The very narrow outermost part of the sixth lateral saddle separates this auxiliary from the umbilical wall.

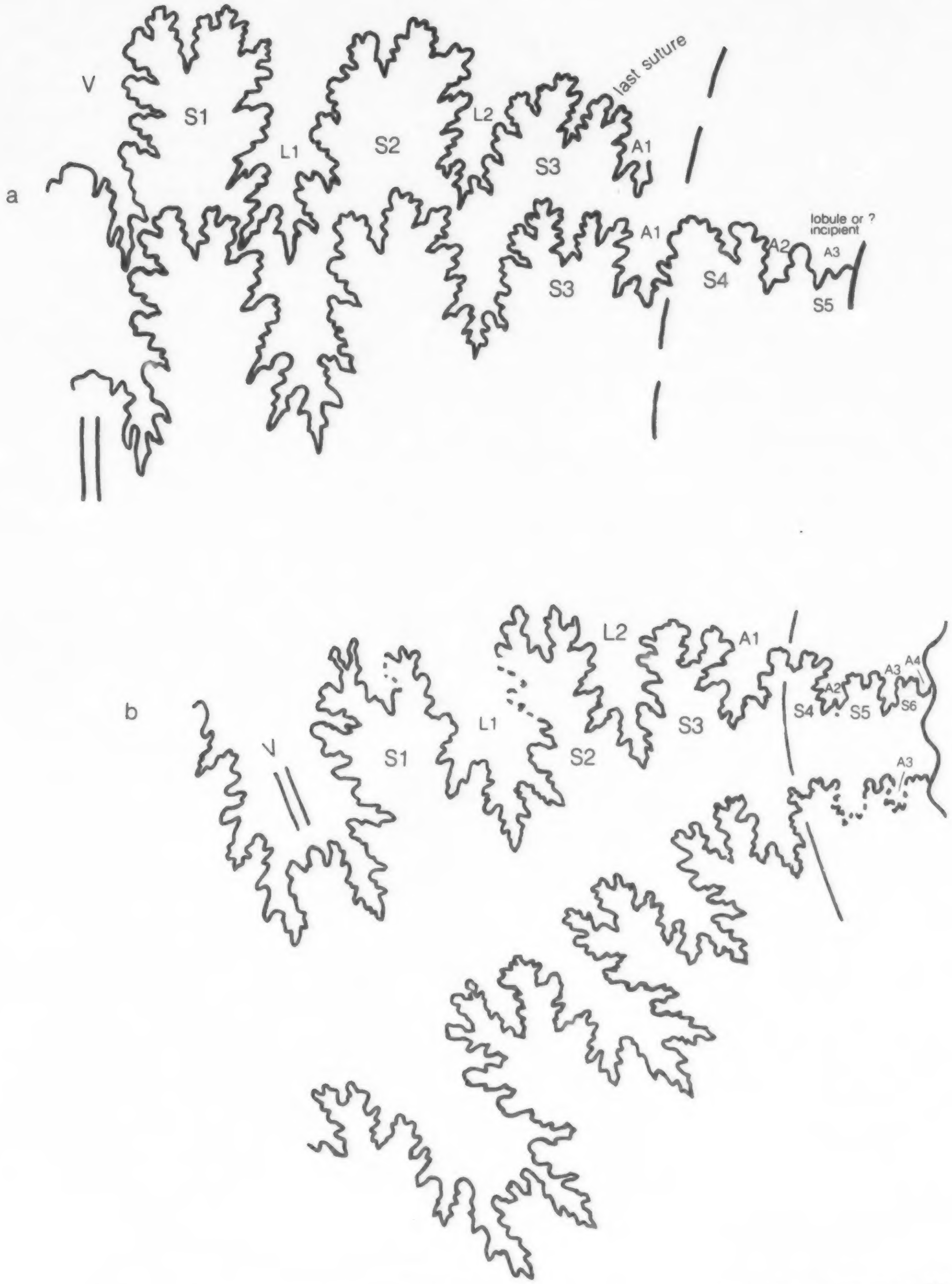
The lateral part of this suture line ending with the first auxiliary lobe is approximately straight and markedly ascendant (at 25 to 30 degrees) in relation to the corresponding diameter. Then it abruptly becomes distinctly suspensive (at 5 to 10 degrees) and remains so to the umbilical seam.

The early adult sutures visible in the specimen BGR, kv 284 (Pl. 9, figs. 4A-4C; Pl. 13, fig. 2; Figure 33b) at the shell diameter of 43 mm are considerably less complexly and deeply denticulated than those of BGR, kv 286. Furthermore, their lobes are appreciably sturdier while their saddles are considerably wider than their counterparts in BGR, kv 286. Except for the presence of three to four well defined auxiliary lobes and the distinctly more slender proportions of all equivalent lobes, the shape, proportions, and the depth of denticulation of these sutures resemble closely those of the suture line of "*Olcostephanus (Polyptychites) bidichotomus*" of Pavlow (in Pavlow & Lamplugh, 1892, Pl. XVI, fig. 3b). The lateral parts of these sutures are also closely comparable with those of *Polyptychites keyserlingi* var. *suessi* (Koenen, 1909, Pl. XII, figs. 2, 3). The orientation of the sutures of BGR, kv 284 is similar to that of BGR, kv 286. In most of these sutures, the short and sturdy (about twice as long as they are wide), distinctly trifid second and third auxiliaries are situated on the umbilical wall. The third auxiliary is separated from the umbilical seam by the exposed greater part of the simply notched sixth lateral saddle, which is twice as wide as this auxiliary. However, in some sutures the fourth auxiliary appears hard at the umbilical seam (Figure 33b). This very sturdy lobe is about as long as it is wide, roundtipped, and but slightly notched on the flanks; its size is about one-third that of the third auxiliary.

The unfigured advanced adult sutures of BGR, kv 279 preceding its presumably late intermediate living chamber at the shell diameter of about 112 mm exemplify the other morphological extreme of the progressive variant. All lobes of these sutures resemble those of the holotype of *P. hapkei* in their short and sturdy proportions combined with a sparse and shallow denticulation (see Figure 33a). However, these lobes are characteristically constricted at the top and their symmetrically to almost symmetrically trifid terminal branches spread sidewise more than do those of the holotype.

The saddles of kv 279 are just as sparsely and shallowly denticulated as those of the holotype. Furthermore, they are either about as wide as or only insignificantly more narrow than those. However, they tend to have forward convex tops and to narrow (instead of widen) adapically because of the shape of flanking lobes. These sutures have three auxiliary lobes, of which the first auxiliary is situated on the lower flank at about the branching point of the primaries. The second and third auxiliaries are sturdy and short, adapically tapering and only slightly serrated. The second auxiliary is situated at the middle of the umbilical wall while the third is situated at the very umbilical seam. The size of auxiliaries decreases (as is also that of the lateral lobes) evenly adumbilically.

The lateral part of the suture line of kv 279, ending with the third lateral saddle, is approximately straight and ascends only moderately (at 10 to 15 degrees) toward the umbilicus. It turns around gradually in the adumbilical part of that saddle and becomes first subradially oriented on the shoulder and then distinctly (at 5 to 10 degrees) descendant on the umbilical wall.


a
V
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S1
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A3

Figure 33. Adult external suture lines of *Polyptychites hapkei* n. sp. **a**. Holotype, BGR, kv 285, reproduced in Pl. 10, fig. 3 (see there for the locality). Two oralmost sutures immediately preceding the adult living chamber at the whorl height (wh) of about 34 mm, x 2. **b**. Specimen BGR, kv 284 reproduced in Pl. 9, fig. 4 (see there for the locality). Early adult suture observed at the whorl height (wh) of about 21 mm of this intermediate whorl, x 5 (approx.).

Though representative of the advanced variant of the suture in the number of auxiliary lobes, the suture line of kv 279 is otherwise morphologically transitional between the conservative and the advanced variants.

The sculpture is, as a rule, coarse. However, there are subordinated variants with more refined sculpture (e.g. BGR, kv 279). A very early appearance of typical bullae is characteristic. These are already present at a shell diameter of 15 mm. Specimen BGR, kv 284 (Pl. 9, fig. 4A) has 16 bullae per whorl at a shell diameter of 50 mm. These bullae are distinctly elevated and extend onto the umbilical wall. In this growth stage the bullae are only slightly comma-like and disappear approximately in the middle of the umbilical wall. The number of the bullae does not change materially in the adult growth stage (about 15 per whorl) where they become still more strongly expressed on the living chamber. However, the strength of the bullae decreases immediately before the mouth border and they simultaneously lose their typical shape. The extensions of bullae on the umbilical wall show a relatively stronger comma-like bend in the intermediate and adult growth stages. Here the bullae peter out within the inner third of the umbilical wall.

The characteristic feature of the sculpture is the presence of 4 to 5 secondary ribs per bundle at a shell diameter of 30 mm (Pl. 9, fig. 4A). The typical quasi-trivirgatitpartitous rib bundles, which are characteristic of older *Polyptychites* forms, are either not present in *P. hapkei* or restricted to its still unknown earliest growth stages. The subdivision points of the secondaries are situated at different levels in the earliest visible rib bundles. The anterior secondary rib splits into two tertiary ribs rather high on the flank. The three posterior secondaries form either a trivirgatitpartitous group or a trifurcate group with obscure subdivision points in the proximity of the bulla. The secondary and tertiary ribs only begin to differentiate at this stage. The tridichotomous bundling habit, which is very characteristic of the intermediate growth stages and exhibits a clear differentiation of the secondary and tertiary rib groups, makes it first appearance at a shell diameter of about 60 mm (Pl. 11, fig. 1A). This bundling habit is rather regular in most representatives of the species. The bidichotomous rib bundles occur relatively rarely. Furthermore, bundles may occur rarely which include an additional tertiary rib which mostly splits up in a rather addorsal position off the anterior secondary rib.

The basically tridichotomous bundling habit remains clearly discernible even when its irregularities become unusually common. In such cases it is common for only 2 of the 3 secondary ribs to arise directly from the bullae. The third secondary rib then occurs either in the middle or on either end of the bundle with no connection to it. When it occurs in the middle of the bundle, it can be connected with the posterior secondary rib (Pl. 10, fig. 3). In that case a bundling habit results, which is similar to that described and figured by Pavlow (in Pavlow and Lamplugh, 1892, Pl. 15, fig. 4a) for *P. triplodiptychus*. The number of ribs is, as always, reduced in the adult. In this case, this stage is dominated by irregularly bidichotomous rib bundles.

Affinities and differences. The morphology and stratigraphic position of *P. hapkei* indicate that this representative of the late *Polyptychites* species group evolved from the *P. keyserlingi* stock, presumably via the poorly known *P. sphaeroidalis*. The essentially *P. keyserlingi*- and *P. sphaeroidalis*-like adult external suture line of *P. hapkei* is particularly diagnostic of its ancestry (Figure 11). Furthermore, the morphology of the suture line of *P. hapkei* indicates that the similarity of its sculpture and whorl shape to those of some representatives of the *Polyptychites multicostatus* species group is a matter of homoeomorphy only.

P. hapkei has a variable shell shape, which tends toward a broad, almost *Euryptychites*-like whorl in the intermediate and adult growth stages. The great variability of the shell shape of *P. hapkei* is strongly reminescent of that existing in *Euryptychites diplotomus*, the root form of true *Euryptychites* of the early early Valanginian. *P. hapkei* seems to play a comparable role among the advanced *Polyptychites* forms in the late early and early late Valanginian. This species appears to be the root form of at least some of the species of the second "*Euryptychites*" — phase (i.e. of *Hollwediceras* n. gen.) in the late early and early late Valanginian.

Because of the ontogenetic development of its whorl shape and the morphology of its adult external suture line (especially of its advanced variant; compare Figures 33b; 36c with Figures 34a, 34b) the species is morphologically, and apparently phylogenetically, transitional between the *P. keyserlingi* species group and the late *Polyptychites sphaericus* species group that is separated below as *Hollwediceras* n. gen. At least one of these *Euryptychites*-like species — *H. praelatus* (Koenen) — has evolved from *P. hapkei* and the same is probably true of *H. sphaericus* (Koenen). These two species have still broader whorls than *P. hapkei*. Furthermore, their umbilical shoulder is acute and their ventral and lateral surfaces are indivisible in advanced and adult growth stages.

The extreme morphological variability of the adult external suture line of *P. hapkei* indicates that it represents a typogenetic evolutionary lineage that develops within the evolutionary center of *Polyptychites*. The general morphology of the advanced variant of this suture line combined with the occasional presence of the fourth auxiliary lobe in at least one of its examples exhibits remarkable similarity to the adult suture of the earliest *Prodichotomites* ex gr. *hollwedensis-polytomus* (compare Figures 36c, 38a-38c). These similarities are interpreted herein as a matter of homoeomorphy (see p. 99 and Figure 11) because these *Prodichotomites* are strikingly similar to *Polyptychites* ex *gr. multicostatus* in their ribbing habit and whorl shape and are connected with that species group by morphologically transitional forms.

The adventral displacement of auxiliary lobes in the early adult suture of kv 284 representing the morphologically and presumably evolutionarily most advanced example of the advanced variant makes this particular suture more similar to the early and advanced adult suture lines of *Polyptychites tschekanovskii* Pavlow and *P.* aff. *tschekanovskii* Pavlow than the rest. In these high Boreal forms, that are direct descendants of *P. hapkei*, the first auxiliary lobe is situated still farther adventrally on the flank while the second auxiliary is situated exactly on the umbilical shoulder (Pl. 35, fig. 1A, 1C; Pl. 41, fig. 1; Figure 48a). These morphological relationships suggest that the inferred transmutation of *P. hapkei* into *P.* ex gr. *tschekanovskii* followed the proterogenetic evolutionary mode, at least where the evolution of the suture line is concerned.

From the almost homoeomorphic *Polyptychites orbitatus* Koenen, *P. hapkei* differs in the lower and broader, more pronouncedly *Euryptychites*-like whorls of its intermediate and adult growth stages and a coarser sculpture. Furthermore, its generally *P. keyserlingi*-like adult external suture line may occasionally be similar to that of *P. orbitatus*. *Polyptychites saxonicus* is more slender and has a denser sculpture with a greater number of tertiary ribs. Its adult external suture line is generally unlike that of *P. hapkei* but may become homeomorphically similar in some rare instances. From the closely allied *P. keyserlingi* species group *P. hapkei* differs, in particular, in the prevalence of tridichotomous rib bundles in its intermediate and adult growth stages. These rib bundles occur only very rarely (e.g. Koenen, 1909, Pl. XIV, fig. 1) in this older *Polyptychites* species. As already mentioned, the adult external sutures of the two species cannot be reliably distinguished, except in the extreme examples of the advanced variants.

P. hapkei, which is restricted to the late early and early late Valanginian, has an exceptionally wide geographical range. It extends from eastern England, the Lower Saxony Basin and middle Europe to Spitsbergen and North Siberia. A closely allied or possibly specifically identical form occurs in the latest early or earliest late Valanginian rocks of the Sverdrup Basin at GSC loc. 82695 (see p. 120, Pl. 43, fig. 2).

Polyptychites triplodiptychus Pavlow 1892

*1892 *Olcostephanus (Polyptychites) triplodiptychus* Pavlow (in Pavlow and Lamplugh), p. 480, Pl. 15, figs. 4a-4c).

Discussion. This is a doubtful species, as no other specimen has been found so far that could be placed in it. The sculpture resembles closely that of *P. hapkei*. However, that species has considerably broader whorls and a wider umbilicus. The sculpture of *P. triplodiptychus* is considerably coarser than that of the otherwise similar *P. orbitatus*. There is little doubt that *P. triplodiptychus* is a representative of the late *Polyptychites* species group, closely allied to *P. orbitatus* and *P. hapkei*.

Polyptychites villersensis Baumberger 1908

*1908 *Polyptychites villersensis* Baumberger, p. 26-29, Text-figs. 131-133.

Discussion. The unique holotype resembles up to a point of *P. hapkei*, which suggests that these two species are allied. They differ, however, in that *Polyptychites villersensis* has a peculiar, triangular whorl shape. A definitive conclusion about their relationship will only be possible when additional specimens become available.

Polyptychites? *multiplicatus* (Roemer 1840/41)

*1840-41 *Ammonites multiplicatus* Roemer, p. 86, Pl. 13, figs. 3a, 3b.

non 1881 *Olcostephanus multiplicatus* Neumayr and Uhlig, p. 150, 151, Pl. 33, figs. 2, 2a, 2b.

?1902 *Polyptychites multiplicatus* Koenen, p. 115, 116, Pl. 3, figs. 4, 5, 9.

Discussion. Plaster casts of Roemer's (1840-41) original from Bredenbeck are preserved in the collections of the Geological Institute, Goettingen and the BGR in Hannover (kv 287). They prove that Roemer's (1840-41, Pl. 13, figs. 3a, 3b) figures are inaccurate and totally misleading. The shell is so laterally deformed and squashed that it is no longer possible to recognize its original shape. It is nevertheless obvious that the shell does not belong to *Olcostephanus*. It is instead either a late *Polyptychites* or an early *Prodichotomites*. However, it is impossible to define the diagnostic features of this species with a sufficient exactitude, so the name "*A.*" *multiplicatus* Roemer should not be used.

Genus *Hollwediceras* nov. gen.

Type species. *Polyptychites sphaericus* Koenen 1902.

Derivation of name. From the locality Hollwede, which has yielded the majority of representatives of the genus.

Diagnosis. The *Euryptychites*-like representatives of Polyptychitinae occurring in the late early and early late Valanginian and characterized by numerous bullae and by subdivision points of the ribs situated rather high on the flanks. Their rib bundles include at least 2 dichotomous elements, which bifurcate at approximately the same level. An additional solitary secondary rib is present in the bundles of intermediate growth stages. This solitary secondary may occupy a very different position in the bundle. The external suture line is similar to the advanced variant of the *P. hapkei* suture; it is characterized by particularly slender, long and strongly denticulated lobes and partly widened saddles.

Discussion. As already mentioned in the description of *Euryptychites*, the upper lower and lower upper Valanginian rocks of Northwest Germany contain *Euryptychites*-like polyptychitinids, which cannot be assigned to the true *Euryptychites* of the lower lower Valanginian. They are a younger, phylogenetically independent, homeomorphic group of forms, which must be given the new generic name *Hollwediceras*. These forms are interpreted herein, as an offshoot of the *Polyptychites sphaeroidalis-hapkei* species group (*see* p. 85 for further details). The *sphaeroidalis-hapkei* species group has, therefore, the same genetic relationship with *Hollwedi-*

ceras as the early early Valanginian *E. diplotomus* has with true *Euryptychites* species.

Hollwediceras is represented in Northwest Germany by *H. sphaericus* (Koenen 1902) and *H. praelatus* (Koenen 1902). These younger species differ from the true early Valanginian *Euryptychites* also in the tridichotomous appearance of the rib bundles (contrasting with the bidichotomous and fasciculate bundles of the true *Euryptychites*) at least in the intermediate growth stages. This further indicates that they represent a lineage that is independent of the true *Euryptychites* and is only convergent to it (Figure 11).

The sculpture of *Hollwediceras* varies considerably. One extreme is the dense and fine sculpture of a typical *H. sphaericus*, which is characterized by a combination of a refinement of the individual sculptural elements with their distinct prorsiradiate orientation. The other extreme is represented by *Hollwediceras praelatus* (Koenen, 1902, Pl. 55, figs. 1, 2), characterized by a radial orientation of coarser ribs.

The characteristic features of the *Hollwediceras* sculpture are particularly well displayed by *Hollwediceras praelatus*. The subdivision of secondary ribs occurs there very high on the flank and all branching points are situated at approximately the same level. At the same time no bidichotomous bundles arise here as the bundles are still characterized by the presence of additional, solitary (i.e. not bifircating) secondary ribs. In the typical variant, this solitary rib forms the anterior element of the bundle *(praelatus* sculpture). However, it can also be situated between the two bifurcating secondaries to produce the polyptychous rib bundles. The absence of quasifasciculate, as well as of bidichotomous, bundles in the middle growth stages combined with the presence of at least some bundles characterized by the *praelatus* sculpture is very characteristic of *Hollwediceras*. This feature is an important distinction of the genus from *Euryptychites*. However, the convergence of *Hollwediceras* and *Euryptychites* becomes so great in the adult state that it may be difficult to differentiate the two genera at this growth stage.

The adult external suture line of *Hollwediceras* n. gen. is morphologically more advanced than that of the true *Euryptychites* and is essentially similar to the advanced variant of the *P. hapkei* suture. Because of the prevalent placement of three lobes (i.e. two lateral lobes and the first auxiliary lobe) on the ventral part of its shell and the prevalent presence of three auxiliary lobes this suture belongs to the advanced type of *Polyptychites* suture. Furthermore, its lobes and saddles are, as a rule, much longer and more complexly and deeply denticulated than those of *Euryptychites*. A characteristic example of the *Hollwediceras* suture is provided by *H. praelatus* (Koenen, 1902, Pl. 55, figs. 1-3). These sutures have no less than three lobes (i.e. the two laterals and the first auxiliary) on the flank and at least two more auxiliaries (i.e. the second and the third) on the umbilical wall. The external suture of *H. sphaericus*, discussed and figured below, is considerably more variable in the distribution and number of auxiliary lobes. However, it also belongs to the advanced type of *Polyptychites* suture with three auxiliary lobes and differs markedly from that of *Euryptychites*.

The combined evidence of differences in the bundling habit, adult external suture line and the stratigraphic ranges is ample for the exclusion of the *sphaericus-praelatus* species group from *Euryptychites* and the erection of the new genus *Hollwediceras* for it.

All specimens listed by Spath (1924) under the names *Polyptychites gravesiformis* Pavlow and *P. euryptychoides* Spath are assumed to belong to *Hollwediceras*. This genus includes the largest cadiform ammonites of the Valanginian, which may reach a shell diameter of 250 mm.

Polyptychites juillerati Baumberger 1908 is placed tentatively into the synonymy of *H. praelatus* (Koenen). *Hollwediceras* appears to extend therefore into the Tethyan Realm.

Only the type species *H. sphaericus* (Koenen) will be discussed in detail below as it is the only representative where sufficient material for a re-description is available. In the case of *H. praelatus* (Koenen) the reader is referred to Koenen's (1902, p. 126, 127, Pl. 55, figs. 1, 2) description. "*Polyptychites*" *globulosus* Koenen (1909, p. 19, 20, Pl. 4, figs. 1, 2) is placed in the synonymy of this latter species.

Hollwediceras sphaericus (Koenen 1902)

Pl. 30, figs. 1-3; Figures 34a, 34b

*1902	*Polyptychites sphaericus* Koenen, p. 122-124, Pl. 4, figs. 1-5.
1978	*Euryptychites sphaericus* Kemper, Ernst and Thiermann, p. 17.

Lectotype. The specimen from the collection of Brandes reproduced by Koenen (1902, Pl. 4, figs. 1-5) is selected herewith as the lectotype of *H. sphaericus*. It is in the collections of the Geological Institute of Hamburg University, TK Nr. 15.

Locus typicus. Hoheneggelsen.

Stratum typicum. Basal beds of the upper Valanginian ("Zone of *Saynoceras verrucosum*").

Material. 7 specimens from the basal upper Valanginian of Hollwede and Twiehausen.

Diagnosis. A *Hollwediceras* species in which broad and low, typically *Euryptychites*-like whorls appear already in the early growth stages. Sculpture fine and dense. Bullae delicate and numerous, numbering about 24 per whorl in the intermediate growth stages. The secondary ribs subdivide rather high on the flank so that the secondary and tertiary ribs are clearly distinguishable. Intermediate growth stages are ornamented with rib bundles of *praelatus*-type and lack quasifasciculate bundles. The adult external suture line appears to be indistinguishable from that of *P. hapkei*.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh I	wh 2	wth 1	wth 2
BGR, kv 364	86	29(33)	26(30)	32(37)	—	—
BGR, kv 365	80	27(34)	26(32)	27(34)	48	63

Description. All representatives available are wholly septate so that the size of an adult shell remains unknown. A large fragment remains septate to a shell diameter of 180 mm. Therefore, this specimen must have reached a minimum size of 230 mm. The real adult size was probably considerably greater than that.

The whorl section varies from that with extremely *Euryptychites*-like proportions (Pl. 30, fig. 3B) to shells with higher and less obtusely rounded whorls. The *Euryptychites*-like whorl shape is already present at the shell diameter of 30 mm, and probably appears considerably earlier than that. However, there was no opportunity to study juvenile whorls. The whorls may become relatively higher in the more advanced growth stages (e.g. BGR, kv 368). The umbilical shoulder is rather acute. The umbilical wall is oriented rather steeply in the extreme *Euryptychites*-like variants. However, it is rather oblique in relation to the plane of symmetry in other relatively higher whorled variants. The moderately wide umbilicus is therefore funnel-like rather than step-like.

The advanced to adult external suture line is extremely variable where the number of auxiliary lobes, width of saddles and the distribution of lobes and saddles on the shell surface are concerned. This variation matches closely that observed in *P. hapkei* n. sp. For example, in the specimen BGR, kv 364 (Figure 34a) only two lateral lobes are situated on the flank. They are followed by an exceptionally wide third lateral saddle that occupies the rest of the flank and the umbilical shoulder. This saddle, which is 2 1/2 to 3 times wider than the second lateral lobe, is followed by the stubby and short first auxiliary lobe that occupies the outer part of the umbilical wall. The next following fourth lateral saddle is, in contrast to the third, exceptionally narrow; its width is less than half of that of the first auxiliary lobe and the two lobules subdividing its top are simple, tiny notches. The second auxiliary lobe occupies the outer part of the inner half of umbilical wall. It is about as long as the first but only half as wide and parallel-sided. The innermost part of the umbilical wall is occupied by a very narrow and undivided saddle-like structure followed by an only partly exposed, trifid lobe-like structure. The length of the latter is about

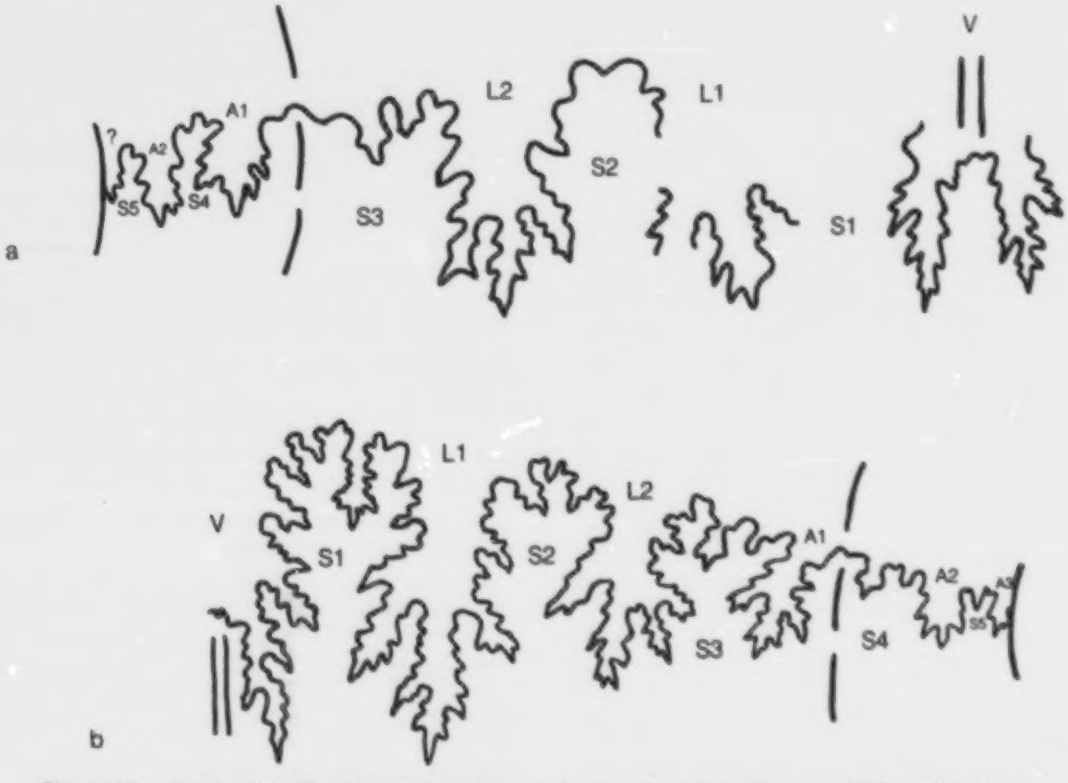

Figure 34. Adult external suture lines of *Hollwediceras sphaericus* (Koenen, 1902). **a.** Specimen BGR, kv 364 reproduced in Pl. 30, fig. 3 (see there for the locality). Early adult suture (incomplete) observed at the whorl height (wh) of 28 mm in this wholly septate specimen, x 2. **b.** Specimen BGR, kv 367. Wiedenbruegge, Northwest Germany. Basal upper Valanginian. A complete early adult suture observed on the last whorl of this wholly septate specimen at the whorl height (wh) of 28 mm, x 2.

two-thirds that of the second lateral lobe. These two structures are interpreted respectively as the underdeveloped fifth lateral saddle and the underdeveloped, only partly exposed third auxiliary lobe. The aberrant, possibly pathological development of the third lateral saddle and the first auxiliary lobe may have been responsible for this underdevelopment. Except for its much lesser denticulation, this suture line nearly duplicates that of the specimen BGR, kv 344 of *P. hapkei* n. sp. (Figure 36b).

In other similarly large specimens exemplified by BGR, kv 367 (Figure 34b) the first auxiliary lobe occurs on the shell's flank distinctly adventrally of the umbilical shoulder. It is slender, long and distinctly constricted at the top. This deeply denticulated, asymmetrically trifid auxiliary has a perfectly normal appearance. Like the long and slender, deeply and richly denticulated first and second lateral lobes it is similar to the equivalent lobes of *Hollwediceras praelatus* (see Koenen, 1902, Pl. 55, fig. 1). It is this auxiliary (instead of the second lateral lobe in kv 364; Figure 34a) that is followed by an exceptionally wide saddle that spans the umbilical shoulder and the outer half of the umbilical wall. The flat top of this fourth lateral saddle is subdivided by three lobules, the middle of which is considerably larger and symmetrically trifid. The following second auxiliary lobe occupies the outer part of the inner half of umbilical wall. It is sturdy (only slightly longer than wide), parallel-sided and simply notched; its tip is symmetrically trifid. The fifth lateral saddle occupies most of the innermost umbilical wall and is only slightly wider than the second auxiliary lobe. Its flat top is subdivided in two by a simple tax-like lobule attesting to its nature and normal development. This saddle is followed by the third auxiliary lobe that occurs at the very umbilical seam. It is about half as long as the second auxiliary but its width comprises less than one-third of that. Its tip is trifid. No part of the sixth lateral saddle is exposed. This suture matches closely that of the specimen kv 286 (Figure 36c) of *P. hapkei* n. sp.

The above described external sutures of the specimens kv 364 and kv 367 differ so strongly morphologically that one would have to think of them belonging to different species of *Hollwediceras*, except that about the same range of infraspecific variation of the suture occurs in *P. hapkei* n. sp. Therefore, and as the material available is too scarce for a defintive decision, the writers prefer to treat these sutures as conspecific. It is, furthermore, necessary to determine whether or not these farreaching differences could have been caused by a pathology or sexual dimorphismus. The exernal suture of kv 367, with its long, narrow and deeply denticulated lateral lobes, etc. is considered to be typical of *Hollwediceras sphaericus*.

The sculpture is relatively delicate and dense. The numerous primary elements form delicate bullae. In the intermediate growth stages they number about 24 per whorl. In the most advanced growth stages known their number decreases to about 20. Their extensions on the umbilical wall peter out within its external third. These extensions are feebly bent forward.

Each of the bullae splits into 2 to 3 secondary ribs, which only bifurcate higher on the flank. The secondary and tertiary ribs are, therefore, clearly differentiated. The branching points of secondaries are commonly, but not always, situated at the same level. The ribbing consists of bidichotomous bundles until a shell diameter of about 40 mm. However, no data are available about the ribbing habit of specimens with shell diameters less than 30 mm. Additional ribs appear beginning with a shell diameter of 40 mm. These ribs occur either between or within the bundles. This may result either in the formation of very typical *praelatus*-like bundles (i.e. bundles with an undivided anterior secondary and two dichotomous secondaries behind it) or in that of true polyptychous bundles with 5 or 6 supplementary ribs. The subdivision points of bifurcating secondaries of this growth stage are situated at about the same level. This bundling habit is the opposite of the fasciculate bundling habit. However, quasifasciculate rib bundles may occur in the latest known ontogenetic stages of *Hollwediceras sphaericus*, which results in their pronounced similarity with those of *Euryptychites* species.

Affinities and differences. As already mentioned, *H. sphaericus* is a direct derivative of the *Polyptychites sphaeroidalis-hapkei* species group, from which it differs in its typically *Euryptychites*-like whorl proportions, beginning with the juvenile growth stages. The intermediate and advanced growth stages of the two can be very similar. However, even in these growth stages the whorls of *H. sphaericus* are lower, and accordingly more *Euryptychites*-like, while its sculpture is more delicate and denser. Furthermore, the sculpture of *H. sphaericus* is less tridichotomous than that of the *P. sphaeroidalis-hapkei* species group. It is characterized, instead, by rib bundles of the *praelatus*-type.

Euryptychites diplotomus does not possess the extreme *Euryptychites*-like cross-section. Furthermore, its primary elements are either non-bullate or but slightly bullate. The sculpture of *E. diplotomus* varies from finely ribbed with quasifasciculate bundles to more coarsely ribbed with exclusively bidichotomous bundles.

Of the older, true *Euryptychites* species, *E. latissimus* resembles *H. sphaericus* most closely. However, it has considerably fewer primary ribs per whorl. Furthermore, the primaries of *E. latissimus* are considerably higher and more strongly developed in the intermediate growth stages and its sculpture is, generally speaking, coarser and less dense than that of *H. sphaericus*. The subdivision of secondary ribs of *E. latissimus* takes place in the proximity of the bullae. This results in the formation of approximately fasciculate rib bundles, at least on its intermediate and adult growth stages. The secondary and tertiary ribs of *E. latissimus* are, therefore, not clearly differentiated, contrary to those of *H. sphaericus*. Finally, this (and all other) *Euryptychites* species has a conservative polyptychitinid external suture line that combines a great width of lateral saddles with broad and stubby, downward tapering shape of lateral and auxiliary lobes, the presence of only two lateral lobes on the flank and that of only two auxiliaries on the umbilical wall.

Genus *Prodichotomites* Kemper 1971

Type species. Polyptychites polytomus Koenen 1902.

Diagnosis. Predominantly large Polyptychitinae species with more or less convex and never subparallel flanks. The flanks clearly converge adventrally even when they are only feebly convex. The sculpture is characterized by refined but clearly defined bullae, the number of which per whorl does not substantially decrease in the course of ontogeny, including the proximity of adult mouth border. The sculpture is relatively fine and dense beginning with the early growth stages. The bundling habit of the intermediate growth stages is irregular and heteroptychous with variable levels of subdivision points. A rib bundle consists of at least 5 but mostly 6 to 7 supplementary (i.e. secondary and tertiary) ribs on the ventral shoulder. Nearly all lineages of the genus are characterized by a tendency to a weakening of the sculpture on the flanks in the late growth stages. This results in a *Neocraspedites*-like appearance of near adult and adult representatives. Constrictions are characteristically absent. The adult external suture line invariably exhibits at least three, and sometimes four, auxiliary lobes and is advanced polyptychitinid in that sense. However, the length, width and shape of all external lobes and saddles vary greatly. One extreme features stubby and broad, adapically tapering, relatively sparsely and shallowly denticulated saddles resembling those of the early representatives of *Polyptychites*. Another extreme features *Polyptychites saxonicus*-like sutures with long and narrow, relatively complexly and deeply indented lobes which are combined with relatively wide but more sparsely and more shallowly denticulated saddles.

Discussion. *Prodichotomites* was erected (as a subgenus of *Dichotomites*) after Kemper (1971) had realized that *Dichotomites* Koenen 1909 (type species *Ammonites bidichotomus* Leymerie in d'Orbigny 1845) is a composite taxon that includes many different species. In *Prodichotomites* he united those species which have convex flanks as well as a fine and dense sculpture. Their adult rib bundles are heteroptychous (see Figure 6) and include many individual elements. Furthermore, they exhibit a widespread tendency to develop a *Neocraspedites*-like terminal growth stage. The species belonging to this group of forms are widespread in the earlier late Valanginian of Northwest Germany, that is in those beds where *Dichotomites sensu* Kemper 1971 is still absent. Hence, Kemper (1. cit.) inferred that *Prodichotomites* is an ancestor of *Dichotomites* and should be treated only as a subgenus. It is difficult to evaluate their phylogenetic relationships from the Northwest German material because this consists almost exclusively of the last whorls. However, some new finds of the early whorls of *Dichotomites* made recently permit one to make important observations about its ontogeny and necessitate a revision of the above interpretation. A comprehensive account will be published elsewhere. However, the following brief remarks must be made here. *Prodichotomites* and *Dichotomites* are obviously two entirely independent lineages that become homoeomorphic only in their last growth stage, which may make difficult their defintive differentiation. Namely, *Prodichotomites* is densely sculptured and has a great number of secondary ribs beginning with its early ontogenetic stages (see for example Pl. 20, figs. 3, 4). This refined, dense and irregular sculpture contrasts strongly with that of *Dichotomites*, the early growth stages of which are distinguished by relatively smaller number of larger sculptural elements. The development of these sparsely ribbed bundles proceeds, as a rule, proterogenetically, starting from the bidichotomous type. Furthermore, the bundling of *Dichotomites* is very regular and follows a trivirgatitpartitous, bidichotomous or tridichotomous mode. Finally, *Dichotomites* differs in the tendency to develop subparallel flanks. The sum total of these distinctions produces shells which differ strongly from those of the genus *Prodichotomites*. These distinctions of *Dichotomites* and *Prodichotomites* were not recognized previously. This may have been, in part, because a late representative of *Polyptychites* belonging to the *P. orbitatus* species group was interpreted as *Dichotomites bidichotomus* (Leymerie in d'Orbigny) by Pavlow (in Pavlow and Lamplugh, 1892, Pl. 16, figs. 2a, 2b). This specimen was later refigured in the treatises (e.g. The Treatise and the Osnovy) as *D. bidichotomus*.

The true *Dichotomites* make their first appearance in the lower part of the upper Valanginian in Northern Siberia. In Northwest Germany they appear considerably later in those beds that were defined by Kemper (1978) as the Zone of *Dichotomites crassus* (Figure 11). This earliest appearance corresponds to the "mid-*Dichotomites*-Beds" of the older German literature. Therefore, true *Dichotomites* does not occur at all in the "lower *Dichotomites*-Beds". The above observations imply that *Dichotomites* arose in North Siberia and migrated only later to Northern and Western Europe.[1] Only *Prodichotomites* will be described in the following sections as no true *Dichotomites* have been found in the Sverdrup Basin. The most important *Dichotomites* species of Northwest Germany were described and figured by Kemper (1978).

Prodichotomites forms a separate taxon of Polyptychitinae, which evolved parallel to but independent from the lineages of *Dichotomites*. In *Prodichotomites* evolution proceeded from widely umbilicate forms with low and still relatively thick whorls (i.e. *hollwedensis-polytomus* species group) toward narrowly-umbilicate, discoidal shapes with slender and high whorls. The latter forms *(P. complanatus*; *P. undulatus* and *P. ivanovi*) represent its end development. In the principal lineage that leads toward *P. ivanovi* (Aristov) the size of the shell increases in the course of phylogenetic development. The specimen reproduced in Pl. 25, fig. 1 has a shell diameter of 210 mm and so is a very large individual for the central part of the Lower Saxony Basin. However, an earlier *Prodichotomites* from Bueckeburg 2 has an unusual shell diameter of 430 mm (collection Wiedenroth, Hannover). It is a quite extraordinary specimen, the taxonomical status of which is uncertain. The gigantic species *P. grotriani* (Neumayr and Uhlig) has so far been observed only in the southern marginal facies of the Lower Saxony Basin.

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[1] E. Kemper is alone responsible for all comments and conclusions dealing with the presence of *Dichotomites* s. str. in the *Polyptychites michalskii* zone of North Siberia and its phylogenetic, biostratigraphic and paleogeographic significance. J.A. Jeletzky reserves the judgement about these ideas and leaves open the possibility of publishing his ideas on the subject at a later date.

The rootform of the genus *Prodichotomites* is *P. hollwedensis* Kemper. It evolved from *Polyptychites* ex gr. *multicostatus* Koenen (Figure 11), with which it is connected by transitional forms. The two are also allied by the characteristic absence of constrictions in all presently known European *Prodichotomites*. This transmutation most probably occurred in the Lower Saxony Basin.

The early *Prodichotomites* species have an exceptionally wide geographical range, from the Tethys (i.e. Southeast France; Thieuloy, 1977) to the high Boreal (or Arctic) basins of North Siberia and Canada (Kemper, 1977). An evaluation of some *Prodichotomites* species or specimens described by Thieuloy (1977) from Southeast France and assigned by him to *Dichotomites ("Neocraspedites")* is impossible because they are all represented by juvenile shells only. This applies in particular to the proposed new species *"Dichotomites" ("Neocraspedites") vocontius* Thieuloy. The French material cannot be sufficiently precisely compared with the German material, in which the juvenile whorls are only rarely preserved. However, there is no doubt that this material consists of early late Valanginian *Prodichotomites* species. These forms are most probably conspecific with the Northwest German material and it is possible to place some of the somewhat larger French specimens in the synonymy of the latter.

It is difficult to appraise the Swiss dichotomitid material on the basis of its figures alone. These figures are definitely rather unreliable, especially those of Pictet and Campiche (1858-60). Their material is derived from the area of Sainte Croix in the Swiss Jura Mountains. In spite of the impossibility of determining their specimens exactly at specific level, all of the "neocraspeditid" ammonites from Sainte Croix indubitably are representatives of *Prodichotomites*. They are either conspecific with, or at least closely related to, the German species of that genus.

For example, "*Ammonites bidichotomus*" of Pictet and Campiche (1858-1960, Pl. XLI, figs. 1a, 1b) is most likely comparable with *Prodichotomites polytomus* while the "*Ammonites carteroni*" (non d'Orbigny 1840-42) reproduced in their Pl. XLII, figs. 1-3 probably compares with *Prodichotomites glaber*. Of the ammonites figured by Baumberger (1908), the "*Craspedites*-Fragment" reproduced in Fig. 138 resembles most closely *P. perovalis* (Koenen). Therefore, the Swiss material also demonstrates a wide distribution of *Prodichotomites*, which ranges right into the Tethyan Realm.

As with *Polyptychites*, it is possible to subdivide *Prodichotomites* in several species groups; these are:

1. Group of *Prodichotomites hollwedensis* Kemper and *P. polytomus* (Koenen).

Summary. The rather primitive *Prodichotomites* forms in which relatively wide and low whorls are combined with a wide, step-like umbilicus. The sculpture is moderately fine and dense, ribs are irregularly bundled ("heteroptychous"). Bullae strongly and typically developed and retain their appearance to the mouth border of the shell.

2. Group of *Prodichotomites pfaffi* n. sp. and *P. robustus* n. sp.

Summary. Descendants of *P. hollwedensis* in the early late Valanginian. They have relatively wide whorls and a coarse adult sculpture, the elements of which are either pronouncedly prorsiradiate or incurved. Other features vary within the group. *P. pfaffi* is very widely umbilicate, has low whorls and is densely ribbed. It still has a *Polyptychites*-like appearance. *P. robustus* is narrowly umbilicate and has only a few bullae.

3. Group of *Prodichotomites flexicosta* (Koenen) and *P. complanatus* (Koenen).

Summary. An early late Valanginian offshoot, which is derived from *P. hollwedensis*. It is characterized by an increased weakening of the sculpture on the flanks which results in a *Neocraspedites*-like appearance. The whorls become relatively more slender and higher and the umbilicus very narrow. However, the umbilicus becomes more evolute again in the late ontogenetic stages. *P. fissuratus* and *P. undulatus* are similar (and perhaps synonymous). However, they retain irregularly developed secondary ribs on the flanks.

4. Group of *Prodichotomites glaber* n. sp.

Summary. An early late Valanginian offshoot of the *P. polytomus* stock which combines a large size with relatively wide whorls and a narrow umbilicus. It has a *Neocraspedites*-like appearance in the adult state.

5. Group of *Prodichotomites perovalis* (Koenen) and *P. ivanovi* (Aristov).

Summary. The principal lineage of the subgenus, which leads to ever larger and more slender shells. The umbilicus becomes ever more narrow in the course of its phylogeny because of an increasing enclosure of the preceding by the succeeding whorls. Contrary to that in Group 3, the umbilicus does not become relatively more evolute in the adult. The *Neocraspedites*-like appearance of the penultimate and ultimate whorls increases in the course of phylogeny parallel with the other above mentioned features.

Prodichotomites polytomus Koenen 1902

Pl. 18, fig. 2; Pl. 19, fig. 2; Pl. 20, fig. 1; Figures 35, 36a

1881	*Olcostephanus Grotriani* Neumayr and Uhlig, p. 153 (in part), Pl. 23, fig. 1 (non Pl. 24, fig. 1).
*1902	*Polyptychites polytomus* Koenen, p. 88, 89, Pl. 46, figs. 3, 4.
1902	*Polyptychites ramulosus* Koenen, p. 89-91, Pl. 46, figs. 1, 2.

?1976 *Dichotomites (Prodichotomites)* juv. ex gr. *ramulosus-polytomus* Kemper, Pl. 27, fig. 9.

1977 *Dichotomites (Dichotomites)* cf. *ramulosus* Thieuloy, p. 417, Pl. 7, fig. 10.

Holotype. The original of Koenen's (1902) Pl. 46, figs. 3, 4 preserved in the collections of GIG, No. 457-26.

Locus typicus. Stadthagen.

Stratum typicum. "Lower *Dichotomites*-Beds" or previous literature (lower, but not the basal, Upper Valanginian).

Material. 9 specimens in collections of BGR in Hannover from Hollwede and Wiedenbruegge.

Diagnosis. A medium-sized species with a relatively thick shell and a sculpture that is coarse and rather irregular. The ribs either do not become reduced or are but slightly reduced on the flanks. Bullae typically developed and numerous. The width of the umbilicus and the height of whorls show considerable variation. The umbilicus is step-like. The adult external suture line varies from the one similar to that of *Polyptychites hapkei* to the one similar to that of the ancestral *Prodichotomites hollwedensis*.

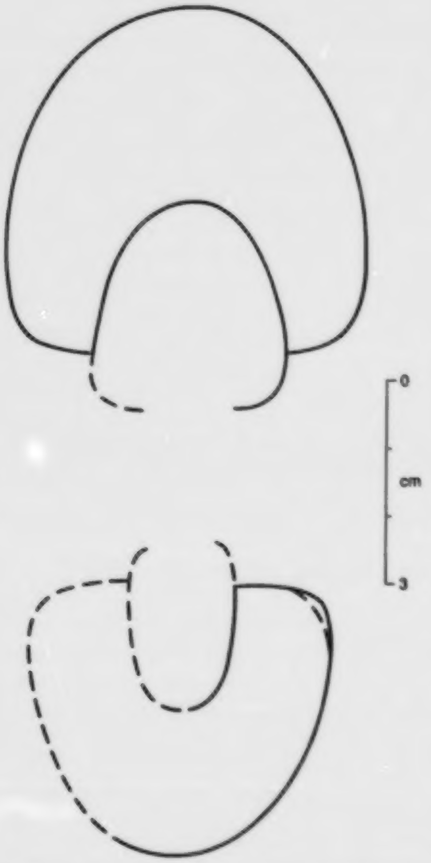


Figure 35. Cross-section of *Prodichotomites polytomus* Koenen, 1902. BGR, kv 289 from Hollwede, Northwest Germany. Lower, but not the basal, upper Valanginian. Note the linear scale.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
BGR, kv 125	113	35(31)	36(32)	43(38)	38	47
BGR, kv 126	128	32(25)	43(34)	53(41)	41	50
BGR, kv 288	90	22(24)	31(34)	37(41)	29	37
BGR, kv 289	123	34(28)	39(32)	50(41)	—	53

Description. The size of the species averages 150 mm. Although the holotype is laterally deformed, it is evident that it belongs to the thick *Prodichotomites* forms. Furthermore, it belongs to the more narrowly umbilicate variants of the species. The same applies to the specimen which was figured by Koenen (1902, Pl. 46, figs. 1, 2) as *Polyptychites ramulosus*. The peculiarities of the sculpture of the latter specimen do not represent specifically diagnostic features as they keep recurring in all species of the *polytomus-ivanovi* lineage. *P. ramulosus* Koenen must be placed accordingly into the synonymy of *P. polytomus*. It is a particularly narrowly umbilicate and thick variant.

The BGR material from Hollwede has, on the average, a broader umbilicus (the umbilical width approximates 26 percent; Figure 35). Specimen kv 125, in which the umbilicus measures 31 percent, represents a broadly umbilicate, extreme variant which connects the species with *P. hollwedensis*. It is also one of those specimens in which wth is greater than wh. In the more progressive variants wh is greater than wth (see the table of measurements). The maximum whorl width is situated at the level of the umbilical shoulder. The flanks are only feebly convex but strongly convergent adventrally. They are, therefore, connected by a narrow ventral arch. The umbilical shoulder is broadly rounded. In the intermediate growth stages it merges imperceptibly into a low and steeply oriented umbilical wall. The umbilical wall becomes higher but less steep in the adult. As the succeeding whorls enclose the preceding ones, at least in the Hollwede specimens, for about 75 percent, the umbilicus is step-like but not funnel-like. The length of the living chamber is one whorl.

The adult external suture lines were only observed in BGR, kv 126 (Pl. 20, figs. 1A, 1B; Figure 36a), the holotype of the species (Koenen, 1902, p. 88, 89; Pl. XLVI, fig. 4) and the holotype of *Polyptychites ramulosus* of Koenen (1902, p. 91, Pl. XLVI, fig. 1), which is here synonymized with *Prodichotomites polytomus*.

The terminal sutures of BGR, kv 126 represent one morphological extreme, which is more similar to some conservative sutures of *P. hapkei* (e.g. Figure 36b) than to the sutures of ancestral *Prodichotomites hollwedensis*. These sutures (Figure 36a) are characterized by relatively

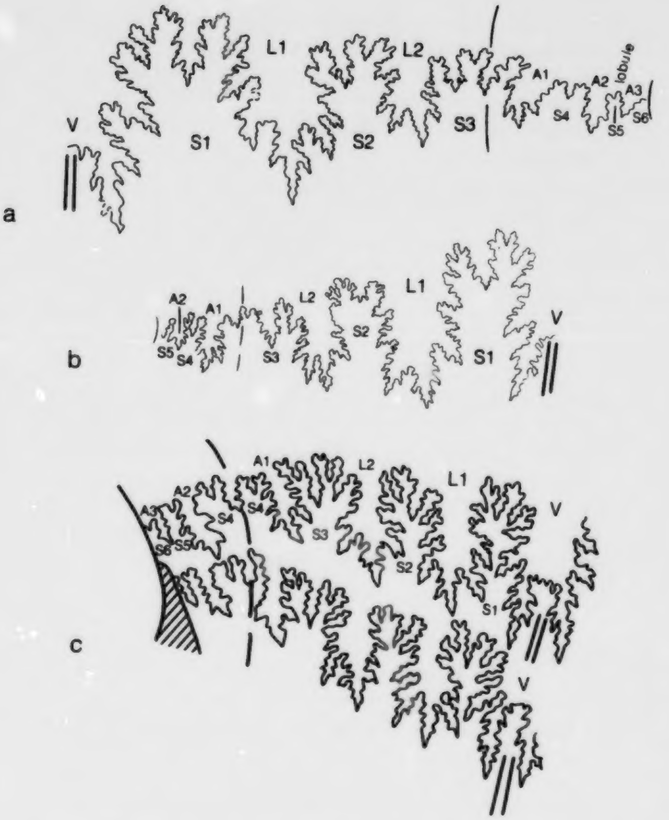


Figure 36. Adult external suture lines of *Prodichotomites polytomus* Koenen, 1902 and *Polyptychites hapkei* n. sp. **a.** *P. polytomus* Koenen. BGR, kv 126 reproduced in Pl. 20, fig. 1 (see there for the locality). Oralmost adult suture immediately preceding the adult living chamber at the whorl height (wh) of 45 mm, x 2. **b.** *Polyptychites hapkei* n. sp. BGR, kv 344 from Hollwede II, Northwest Germany. Uppermost lower or ?basal upper Valanginian, *Prodichotomites hollwedensis* Zone. Second suture from the adult pragmocone's end at the whorl height (wh) of about 36 mm, x 2. **c.** *Polyptychites hapkei* n. sp. BGR, kv 286. The same locality and age as for the specimen BGR, kv 344 (Fig. 36b). Two advanced adult sutures observed at the adult penultimate whorl at the whorl height (wh) of about 34 mm, x1.

sturdy, though distinctly constricted and elaborately denticulated lobes (except for simply denticulated to only notched second and third auxiliaries). These asymmetrically trifid lateral and auxiliary lobes are only 2 1/2 to 3 times longer than wide. Furthermore, these sutures are distinguished by the presence of only two lateral lobes on the flank with all three auxiliaries situated on the umbilical wall. Such distribution of lobes is unknown in *P. hollwedensis* but may occur in the conservative sutures of *P. hapkei* (e.g. Figure 36b), except that the latter have only two auxiliary lobes. The crest of the umbilical shoulder of BGR, kv 126 runs through the middle of uniquely wide third lateral saddle, which is almost three times wider than the preceding second lateral lobe (Figure 36a). Here again, similarly wide and complexly denticulated third lateral saddles are known in *P. hapkei* (Figure 36b) but not in *P. hollwedensis* (Figures 38a-38c). The first lateral saddle of BGR, kv 126 is considerably widened (somewhat wider than the ventral lobe) relatively to any known equivalent in *P. hapkei* and *P. hollwedensis* and widens markedly adapically. Unlike any known example of the conservative suture of *P. hapkei*, the suture of BGR, kv 126 has a normally developed fifth lateral saddle and third auxiliary lobe. However, all its auxiliaries are much more sturdy and less complexly denticulated than their equivalents in any known suture of *P. hollwedensis*.

The above discussed features differentiate the sutures of BGR, kv 126 from the other two presently known suture lines of *P. polytomus*. They also differentiate this suture from all presently known adult external sutures of *P. hollwedensis* (see its description for further details).

The terminal external suture of the holotype of *Prodichotomites polytomus* (Koenen, 1902, p. 88, 89; Pl. XLVI, fig. 4) appears to be morphologically transitional between that of BGR, kv 126 (Figure 36a) and that of its representative previously described as the holotype of *P. ramulosus* (Koenen, 1902, p. 91; Pl. XLVI, fig. 1). Judging by the photograph of this incompletely drawn suture (Koenen, l. cit.), all its four visible lobes (i.e. the two laterals and the first and second auxiliaries) differ from their equivalents in kv 126 in considerably more narrow and slender proportions, subparallel flanks, and symmetrically to subsymmetrically trifid terminations. Their lateral lobules are distinctly shorter and less complexly denticulated. Unlike the BGR, kv 126, three of these lobes are situated on the flank while the second auxiliary lobe is situated on the outermost part of the umbilical wall. All visible saddles of the holotype are subequally wide and one and a half to two times wider than the preceding lobes. In contrast to BGR, kv 126, the third lateral saddle is not appreciably wider than the rest. The lateral lobules of the flanking lobes do not penetrate deeply into any of these saddles, which results in them looking relatively wider. In all above features, the suture of the holotype is similar to the conservative suture of the holotype of *Polyptychites hapkei* (Figure 33a) and the progressive suture of its BGR, kv 284 (Figure 33b).

At the same time, it differs markedly in the same features from the suture of the holotype of "*Polyptychites ramulosus*" Koenen (1. cit.). The close resemblance of this suture to the second variant of *Prodichotomites hollwedensis* suture (Figure 38a) is discussed in its description.

Only two auxiliary lobes are visible in the photograph of the holotype of *P. polytomus* and there is no mention of any additional auxiliaries situated deeper on its umbilical wall in Koenen's (1902, p. 89) description. However, there is ample room for the third auxiliary on the greater, entirely concealed, inner part of this wall and the presence of only one (i.e. the second) auxiliary on the umbilical wall is a rare feature in the Polyptychitinae. It is all but unknown in those forms where the two lateral lobes and the first auxiliary lobe are situated on the flank of the shell. Finally, all presently known examples of adult external sutures of the immediately ancestral *P. hollwedensis* (see its description for further details) possess the third auxiliary lobe. Therefore, the third auxiliary lobe is assumed to be present in the suture of the holotype of *P. polytomus*.

The terminal external suture line of the holotype of "*Polyptychites ramulosus*" Koenen (1902, p. 91; Pl. XLVI, fig. 1) here synonymized with *Prodichotomites polytomus* represents another morphological extreme that is similar to the first variant of adult external suture of *P. hollwedensis* (Figures 36b, 36c) in all its observable features. This suture is just as incompletely drawn as that of the holotype of *P. polytomus* and so is somewhat difficult to appraise definitively from its figure alone.

The visible part of this suture line is similar to that of the holotype of *P. polytomus*.

The sculpture is dense and irregularly-variable. The bullae are slender, as a rule. However, they are typically developed already early in the ontogeny (beginning with a shell diameter of at least 30 mm). They number 19 per whorl and their number does not decrease noticeably in the adult. They become only a little more prominent on the living chamber in comparison with the early whorls. The extensions of the bullae (or those of the primary ribs) on the umbilical wall are oriented radially to the shell at a diameter of 30 mm. Then they develop an increasingly comma-like bend. In the adult these extensions disappear at about the middle of the umbilical wall.

It is a characteristic feature of the sculpture, that not all secondary ribs arise from the bullae. Some of them are intercalated instead. Nevertheless, at least 2 secondary ribs arise from a single bulla; one of these is sometimes more strongly developed than the other. Furthermore, there are other ribs distinguished by a greater strength from other secondary ribs which may either arise from the middle of the bundle (from its anterior or posterior secondary rib) or be simply intercalated therein (Pl. 19, figs. 2A, 2C).

The splitting up of the secondary ribs into tertiary ribs occurs at different levels of the flank, more commonly in a mid-flank zone than very close to the venter. Specimen BGR, kv 288 (Pl. 19, figs. 2A, 2C) with its very adventral and fairly regular subdivision is an exception to this rule and is interpreted as an extreme variant. As in *Polyptychites*, this species group acquires the highest numbers of ribs per bundle on the penultimate whorl and the early half of the last whorl. Here one secondary rib may split into 3 tertiary ribs with different heights of subdivision points *(polytomus*-type). Supplementary tertiary ribs may occur either within or outside the bundle. The sculpture of *P. polytomus*, and that of the younger species derived from it, acquires an irregular character because of the different strength of the secondary ribs and the variable levels at which they subdivide. A reduction in number of ribs sets in, as always, in the adult. The ribs on the flanks remain strong, as a rule, to the very mouth border. Exceptionally, an insignificant weakening may also occur (e.g. BGR, kv 126). In spite of sculptural irregularity, *P. polytomus* obviously represents an evolutionary modification of the tridichotomous sculpture of late *Polyptychites* species.

Affinities and differences. Prodichotomities polytomus has evolved from *P. hollwedensis* and is connected by transitional forms with this species. *P. polytomus* differs first of all in its more narrow umbilicus combined with a greater involution and a greater whorl height. On the other hand, *P. polytomus* is the rootform of the important *perovalis-ivanovi* lineage. Therefore, it is also connected by transitional forms with *P. perovalis*, which is more narrowly umbilicate and has still more slender and higher whorls than *P. polytomus*. *P. glaber* is interpreted herein as a narrowly umbilicate offshoot of *P. polytomus*, which differs from it in the larger size of the shell, a decrease of the number of bullae in the adult, and an early weakening of the sculpture on the flanks. Furthermore, the umbilicus of *P. polytomus* is more step-like and the sculpture is coarser. Finally, its bullae are less comma-like and higher than those of *P. glaber*. *P. glaber* is also thicker than the species of the *polytomus-ivanovi* lineage.

The above described extreme morphological variability of *P. polytomus* suture line appears to be entirely infraspecific in character. The three specimens concerned are typical representatives of the species in all other aspects of their morphology and are derived from the same Lower/Upper Valanginian transition beds (i.e. Hollwedensis Zone). Furthermore, the morphologically extreme, most conservative suture of BGR, kv 126 appears to be connected with the other morphologically extreme, progressive (i.e. entirely *P. hollwedensis*-like) suture of the holotype of "*Polyptychites ramulosus*" Koenen by the morphologically transitional suture of the holotype of *P. polytomus*. Like the extreme variability of the whorl shape and sculpture of *P. polytomus*, this range of variation of its adult external suture apparently reflects the naturally wide infraspecific variation of the rootstock of *Prodichotomites* within its evolutionary center. The similarities of the more conservative sutures of *P. polytomus* to some sutures of *Polyptychites hapkei* are believed to be a matter of homoeomorphy alone.

P. polytomus has been found only in Northwest Germany and Southeast France (Thieuloy; 1977, Pl. 7, fig. 10). However, its geographical range should be considerably wider than that.

Stratigraphic range. According to Kemper (1978, p. 197, Fig. 5), *P. polytomus* is restricted to those beds at Hollwede that overlie beds containing *P. hollwedensis*, *Polyptychites hapkei*, *P. orbitatus*, *Prodichotomites* ex gr. *gradatus-flexicosta*, and *P.* ex gr. *undulatus-complanatus*. It was, therefore, treated as an index fossil of the lower, but not the basal, upper Valanginian beds immediately above the zone of *Prodichotomites hollwedensis* (Figure 62). This conclusion is still valid to the best of the writers' knowledge.

Prodichotomites hollwedensis Kemper 1978

Pl. 16, figs. 1, 3; Pl. 27, fig. 2; Pl. 28, fig. 4;
Figures 37; 38a-38c

1950 "flache Polyptychiten" (pars) Stolley, p. 122, 123.

1977 *Dichotomites (Prodichotomites) hollwedensis* (a nomen nudum) Kemper, p. 4.

1977 *Dichotomites ("Neocraspedites")* cf. *fissuratus* Thieuloy, p. 420, Pl. 8, figs. 2, 3.

1978 *Dichotomites (Prodichotomites) hollwedensis* Kemper Ms. (?) Kemper, Ernst and Thiermann, p. 20, Pl. 1, figs. 4, 5.

*1978 *Dichotomites (Prodichotomites) hollwedensis* Kemper, p. 216-218, Pl. 1, fig. 1; Pl. 2, fig. 1; Pl. 3, figs.1, 2; Figs. 16-18.

Holotype. Original of Kemper's (1978) Pl. 1, fig. 1a, 1b, preserved in Hannover, BGR, kv 118.

Locus typicus. Twiehausen.

Stratum typicum. Lower/upper Valanginian boundary beds, Hollwedensis Zone.

Material. 28 specimens from Hollwede and Twiehausen preserved in collections of BGR in Hannover.

Diagnosis. A medium-sized species with a wide and shallow umbilicus; whorls slender to moderately thick. Sculpture is variable and not strongly developed. However, the bullae are well expressed. The adult external suture line essentially as in younger representatives of the *Polyptychites multicostatus* species group (e.g. *P. saxonicus* n. sp.).

Measurements in (mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
BGR, kv 117	115	33(29)	37(32)	45(39)	—	—
BGR, kv 119	108	26(24)	38(35)	45(42)	34	42
BGR, kv 115	99	26(26)	30(30)	43(43)	31?	—
BGR, kv 120	144	46(32)	43(30)	55(38)	43?	59?
BGR, kv 146	114	35(31)	35(31)	45(40)	—	—
BGR, kv 116	107	30(28)	34(32)	44(41)	—	—

Description. As is evident from the table of measurements, the values of shell measurements exhibit a considerable scatter. To understand this, one must consider that *P. hollwedensis* is the root stock of the genus *Prodichotomites*. Therefore, it is morphologically intermediate between *Polyptychites* and *Prodichotomites* and includes some transitional forms to the ancestral and descendant species. The morphological variability of *P. hollwedensis* is bewildering. Because of the presence of almost all conceivable transitional forms, it cannot be satisfactorily expressed taxonomically. This is a typical infraspecific variability of a rapidly evolving lineage, which experiences a typogenetic phase (Schindewolf, 1947) within its center of evolution. A subdivision into subspecies could perhaps be useful. However, its value is problematical in the present state of knowledge of *P. hollwedensis*.

Kemper (1978) has figured 4 representatives of the species. These specimens give an idea of its morphological properties. The reader is, therefore, referred to these figures and to the description provided in the paper. The specimen figured herein (kv 119; Pl. 16, fig. 1) is an extreme variant. It is relatively narrowly umbilicate and so transitional to *P. polytomus*. Its sculpture is progressive as it differs considerably from the tridichotomous bundling habit of the immediate ancestors and the primitive variants of the species.

Generally speaking, this medium-sized species (average size in order of 140 mm) is characterized by the following features. Most shells are relatively widely umbilicate and have low whorls (Figure 37). The whorl width is small to moderate and its greatest width is situated in the proximity of the umbilical shoulder. The early whorls are, relatively, the most narrow. Therefore, it can be inferred that the development of more narrow, *Dichotomites*-like whorl follows the proterogenetic mode. As compared with the relationships characteristic of *Polyptychites*, the whorls are more slender and less convex. The flanks are feebly convex but converge toward the venter and are connected by a narrowly rounded ventral region.

The enclosure of the preceding whorls by the subsequent whorls is moderate, as a rule. This results in a step-like appearance of the umbilicus. The umbilical wall is low and moderately inclined. The umbilicus is accordingly relatively shallow. The length of the living chamber is approximately equal to that of one whorl.

Five good examples of the external suture of *P. hollwedensis*, which include its early and advanced adult growth stages, are available. These examples include all sutures figured by Kemper (1978, p. 216-218, Pl. 1, fig. 1; Pl. 2, fig. 1; Pl. 3, figs. 1, 2; Figure 18) in the paper where *P. hollwedensis* was originally published.

The adult external suture of the specimen BGR, kv 146 (Kemper, 1978, Pl. 3, fig.2; this paper, Figures 38b, 38c) exemplifies one morphological extreme which matches closely the terminal suture of that representative of *Prodichotomites polytomus* figured as *Polyptychites ramulosus* by Koenen (1902, Pl. XLVI, fig. 1). The two lateral lobes and the first auxiliaries of

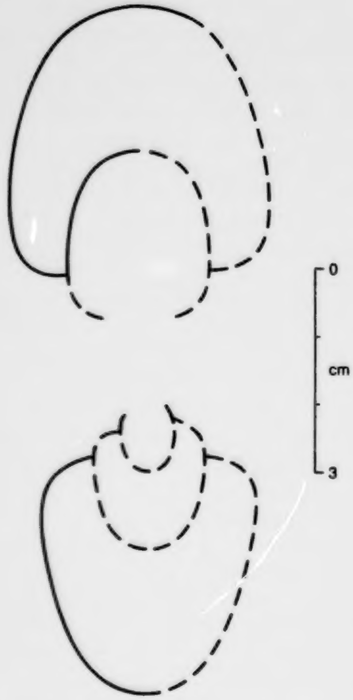


Figure 37. Cross-section of *Prodichotomites hollwedensis* Kemper, 1978. Specimen BGR, kv 194 from Hollwede, Northwest Germany. Lower/upper Valanginian boundary beds, Hollwedensis Zone. Note the linear scale.

these two sutures are essentially similar, except that the first auxiliary of the BGR, kv 146 is somewhat wider and more deeply denticulated. The denticulation of the first to third lateral saddles of the two specimens is also similar. Furthermore, these lobes and saddles are similarly positioned on the flank and similarly wide, except that the third lateral saddle of BGR, kv 146 is appreciably wider than that of Koenen's (l. cit.) specimen.

The invisible ventral lobe of Koenen's (l. cit.) specimen is believed to be similar to that of BGR, kv 146. The latter lobe is only slightly longer and about two times wider than the first lateral lobe. These two lobes of BGR, kv 146 are approximately equally complexly and deeply denticulated. The first auxiliary of BGR, kv 146 is about 4 1/2 times longer than wide, asymmetrically trifid and inclined adventrally at 30 to 35°. The same appears to be true of the Koenen's (l. cit.) specimen.

The fourth lateral saddle spans the innermost flank and the outermost umbilical wall and appears to be equally wide (3 to 3 1/2 times wider than the first auxiliary) in both specimens. However, it appears to be more deeply and complexly denticulated in the BGR, kv 146.

The remaining umbilical part of this variant of the suture is only known in the BGR, kv 146. The second auxiliary lobe occupies most of the outer half of the umbilical wall. It is about two-thirds as long but only half as wide as the first auxiliary and it is considerably more denticulated than the latter. Otherwise the two are similar and comparably strongly inclined adventrally (Kemper, 1978, Pl. 3, fig. 3; this paper Figure 38b).

The relatively very narrow fifth auxiliary saddle occupies the third quarter of the umbilical wall. This saddle is about two times wider than the second auxiliary and subdivided by one tiny, simple lobule. It is strongly underdeveloped in comparison with the normally developed fifth lateral saddle of BGR, kv 145 (Figure 38a).

The very slender and long (4 to 5 times longer than wide) third auxiliary lobe is two-thirds as long as the second auxiliary while being only one-half as wide. Its flanks and tip are only simply and shallowly denticulated, in contrast to those of the second auxiliary. This pronouncedly adventrally inclined third auxiliary may be situated either hard at the umbilical seam or some distance from it. If the latter (Figure 38b), the exposed part of the only shallowly notched sixth lateral saddle is pronouncedly descendant. The third auxiliary and the visible part of the sixth lateral saddle are just as distinctly underdeveloped in comparison with their equivalents in the other extreme variant (e.g. BGR, kv 145; Figure 38a) as is the second auxiliary.

The suture of BGR, kv 146 is slightly ascendant over the two lateral lobes and the first auxiliary lobe. Then it turns over rapidly within the fourth lateral saddle and becomes markedly (10 to 15 degrees) descendant. This descendant orientation then persists to the umbilical seam gradually increasing all the way.

The earlier adult sutures of the specimen kv 146 (Kemper, 1978, Pl. 3, fig. 2) are somewhat less denticulated, their elements are more sturdy and they are relatively more widely spaced (about one-quarter to one-fifth of their height) than those exposed farther adorally. The distance separating the adjacent sutures gradually decreases adorally until the tips of their ventral lobes and those of the first auxiliary lobes begin to touch the tops of the saddles of immediately preceding lines on the last quarter of the whorl, which precedes immediately the adult living chamber. The suture lines become more complexly and deeply denticulated and their lobes are more slender at the same time. The remaining adumbilical parts of these terminal adult sutures remain narrowly separated.

The other morphological extreme of adult external suture line differs in a considerably more shallow and less florid denticulation of its both lateral and the first auxiliary lobes combined with a regularly trifid shape of the first lateral lobe. Another distinction is the relatively much wider proportions and a considerably more complex denticulation of its fifth and sixth lateral saddles. The third auxiliary is also considerably more complexly denticulated, distinctly trifid, and situated farther away from the umbilical seam than in the first variant. This second, apparently morphologically more advanced variant resembles more closely the visible parts of the terminal suture of the holotype of *P. polytomus* described and figured by Koenen (1902, p. 88, Pl. XLVI, fig. 4)

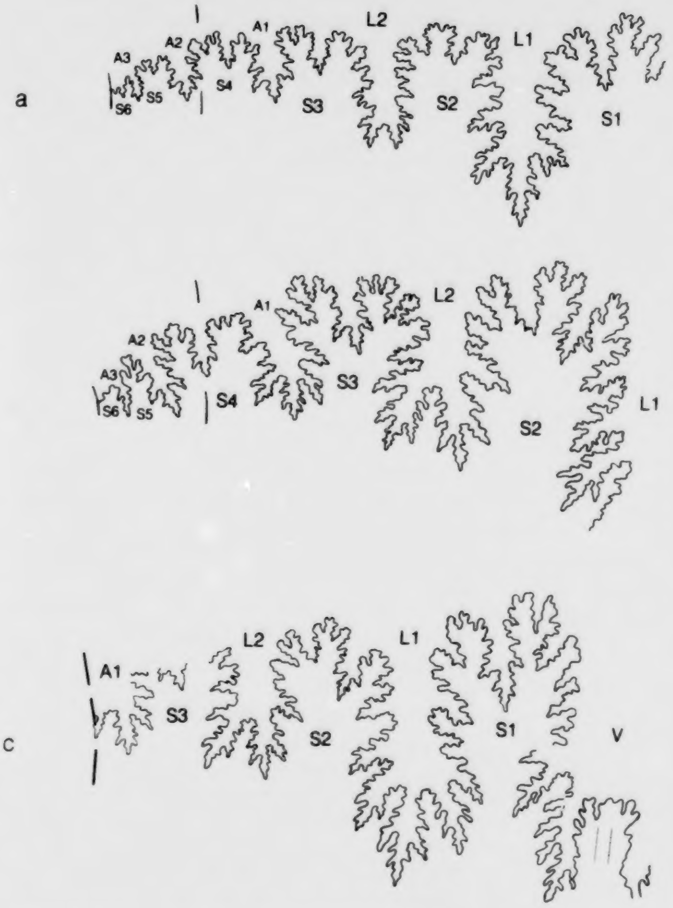


Figure 38. Adult external suture lines of *Prodichotomites hollwedensis* Kemper, 1978. **a**. Specimen BGR, kv 145. Hollwede, Northwest Germany. Lower/Upper Valanginian boundary beds, Hollwedensis Zone. Advanced adult suture exposed on the oralmost one-eighth of adult penultimate whorl at the whorl height of about 38 mm, x 2.5. **b**. Specimen BGR, kv 146. The same locality and age as for the specimen BGR, kv 145. Advanced adult suture observed on the last quarter of adult penultimate whorl at the whorl height of about 40 mm, x 3 (approx.). **c**. An incomplete earlier adult suture of the same specimen as in Figure 36b (BGR, kv 146) observed at the whorl height (wh) of 32 mm, x 4.5 (approx.).

than it does that of its other representative described and figured as *"Polyptychites ramulosus"* by Koenen (1902, p. 90, 91, Pl. XLVI, fig. 1). This variant is much more common in the material studied. It is represented by the sutures of the figured specimens BGR, kv 145 (Kemper, 1978, Pl. 3, fig. 1; Figure 18; this paper Figure 38a), BGR, kv 118 (Kemper, 1978, Pl. 1, fig. 1a) and BGR, kv 117 (Kemper, 1978, Pl. 2, figs. 1a, 1b). The adult external suture lines of the unfigured specimen BGR, kv 327 are morphologically transitional between these two extreme variants, though closer to the second.

The length of the first lateral lobe of the second variant fluctuates between 3/4 and somewhat more than 2/3 that of the ventral lobe. The ventral lobe is parallel-sided, relatively more narrow and much less deeply and complexly denticulated than that of the other extreme variant.

The relatively shallowly denticulated first lateral saddle is considerably wider than that of the first variant. It is from 1 1/4 (in BGR, kv 118) to at least 2 times (in BGR, kv 145; Figure 38a) wider than the ventral lobe and from 1 1/2 (again BGR, kv 118) to almost 3 times (again BGR, kv 145) wider than the first lateral lobe.

The first lateral lobe is much sturdier and shorter than that of the other variant. Its length varies from about four times (in BGR, kv 145; Kemper, 1978, Pl. 3, fig. 2; Figure 38a) to about 2 1/2 times (in BGR, kv 117 and BGR, kv 118; Kemper, 1878, Pl. 1, fig. 1a; Pl. 2, fig. 1b) its width and the flanks are either subparallel or slightly contract adapically instead of being constricted at the top and expanding adapically. The denticulation is considerably simplified and is more shallow in comparison with that of the other variant.

The second lateral saddle either does not differ materially from that of BGR, kv 146 (e.g. in BGR, kv 117 and BGR, kv 118) in its width or is somewhat wider (i.e. about two times wider than the first lateral lobe in BGR, kv 145; Kemper, 1978, Pl. 3, fig. 1). However, its denticulation is always considerably simplified.

The second lateral lobe is again a relatively short and sturdy, only shallowly and simply denticulated structure, the flanks of which are either subparallel or taper slightly adapically. This lobe differs from its equivalent in BGR, kv 146 in the same way as does the first lateral lobe. The length of the second lateral is from 2 1/2 times to 3 times its width in BGR, kv 145 (Kemper, 1978, Pl. 3, fig. 1; Figure 18; this paper, Figure 38a) and 1.5 to 2 times of its width in BGR, kv 118 (Kemper, 1978, Pl. 2, fig. 1a).

The third lateral saddle of the here discussed variant is always similar to that of BGR, kv 146, except for its considerably simplified and more shallow denticulation.

The shape and proportions of the first auxiliary lobe vary strongly from one specimen to another and from one suture line to another in every one of them. It may be almost as slender and long as that of BGR, kv 146 (e.g. BGR, kv 117; Kemper, 1978, Pl. 2, fig. 1a) but is, as a rule, appreciably to considerably sturdier. Furthermore, it is invariably smaller and much less complexly and deeply denticulated than that of BGR, kv 146. The width of the fourth lateral saddle varies from about one-half (e.g. BGR, kv 145; Kemper, 1978, Pl. 3, fig. 1; Figure 18) to about three-quarters (e.g. BGR, kv 117; Kemper, 1978, Pl. 2, fig. 1a) that of the equivalent saddle of BGR, kv 146 (Figure 38b). It is situated entirely on the lower flank in BGR, kv 145 (Kemper, 1978, Pl. 3, fig. 1) but is displaced entirely to almost entirely to the outer third of the umbilical wall in BGR, kv 118. In BGR, kv 117 it straddles the umbilical shoulder (Kemper, 1978, Pl. 2, fig. 1a) just as it does in the BGR, kv 146 (Kemper, 1978, Pl. 2, fig. 2). The denticulation of this saddle is always simplified in comparison with that of the former variant (e.g. BGR, kv 146).

The positioning of the second auxiliary lobe is extremely variable. In BGR, kv 145 it is situated on the umbilical shoulder while in BGR, kv 118 it is situated well within the outer half of the umbilical wall. In the BGR, kv 117, finally, it is situated on the outermost part of the umbilical wall. It is oriented sublongitudinally in the specimens BGR, kv 118 and kv 145 and only in the specimen BGR, kv 117 is it distinctly inclined adventrally as it is in BGR, kv 146 (Kemper, 1978, Pl. 3, fig. 2, Figure 18). This lobe is invariably considerably smaller, sturdier and more simply denticulated than in the other variant (e.g. BGR, kv 146). Its length is about one-half of that in the specimen BGR, kv 146 while the width of the two remains comparable.

The width and positioning of the fifth lateral saddle is rather variable. In BGR, kv 145 it is at least twice as wide as the second auxiliary and spans the inner umbilical shoulder and the outermost umbilical wall, in contrast to its width and positioning in BGR, kv 146 (Figure 38b). This saddle is, furthermore, more richly denticulated in BGR, kv 145, than in BGR, kv 146. In BGR, kv 117 and BGR, kv 118 the width and positioning of this saddle are transitional between those in BGR, kv 145 and BGR, kv 146.

The well preserved third auxiliary lobe of BGR, kv 145 (Kemper, 1978, Figure 18; this paper, Figure 38 a) occurs just before the middle of the umbilical wall. In contrast with the third auxiliary of BGR, kv 146 (Figure 38b) it is a short and sturdy (about 1 1/2 times longer than wide) subparallel-sided, simply notched but apically asymmetrically trifid structure.

The relatively more slender and longer (three times longer than wide) third auxiliary lobe of the specimens BGR, kv 117 and BGR, kv 118 appears to be morphologically transitional between the auxiliary lobe of the specimen BGR, kv 145 and that of BGR, kv 146 in its shape, proportions and orientation. This subparallel-flanked lobe is only slightly denticulated on the flanks and its still trifid tip does not expand like that of BGR, kv 146.

The third auxiliary lobe of BGR, kv 145 is separated from the umbilical seam by the inner half of the umbilical wall. As clearly indicated in Kemper's (1978, Figure 18) drawing, this part of the wall may, sometimes, be ornamented by two small but broad, subtriangularly shaped, only slightly notched lobe-like structures separated from the third auxiliary and from each other by about two times wider, forward-convex topped saddle-like elements. Both of these seem to be true saddles rather than saddle-like embayments separating lobules of a broad saddle as their tops are incised by solitary tiny, sharptipped lobules. The second lobe-like structure occurs at the very umbilical seam. The lobe-like structures appear, therefore, to be true fourth and fifth auxiliary lobes rather than lobules of the sixth lateral saddle. However, these supplementary lobes are only present in the three oralmost sutures of this specimen immediately preceding its adult living chamber. They are definitely absent in all other exposed sutures (six in all) of that half whorl and in those of its inner whorls as well. All these sutures exhibit one, tiny, distinctly notched lobule between the third auxiliary and the umbilical seam (Figure 38a). Nor are these additional auxiliary lobes present in any of the observed ultimate sutures of the specimens BGR, kv 117 and BGR, kv 118, the adult suture lines of which only exhibit one tiny, apparently simple lobule between the third auxiliary lobe and the umbilical seam. The supplementary lobes and saddles of the last three sutures of BGR, kv 145 must therefore be considered as an individual aberation (? a mutation) that occurred at its very last growth stage. It appears to be similar to the previously mentioned examples of disorganization of ribbing habit on the last growth stages of Polyptychitinae.

The orientation of adult external suture lines of the second variant varies considerably. That of BGR, kv 145 is approximately straight and strongly ascendant (at 25 to 30 degrees all the way) either to the middle of the fourth auxiliary saddle or even to the second auxiliary lobe. Then it rapidly turns around and becomes slightly (earlier sutures) to distinctly (later sutures) suspensive to the umbilical seam. However, this suspensive orientation is much less than that in BGR, kv 146 and this is reflected in the either longitudinal or only slightly to distinctly (15 degrees at the most) inclined orientation of the corresponding lobes and lobules. The adult sutures of BGR, kv 117 are oriented as these of BGR, kv 145, except for a somewhat more strongly expressed suspensive orientation of their umbilical parts. This is reflected in a somewhat stronger adventral inclination of their second and third auxiliaries.

The adult sutures of BGR, kv 118 are as strongly or even stronger (?35 to ?40 degrees) ascendant than those of the specimen BGR, kv 145. However, the few exposed umbilical parts of these sutures (beginning with second auxiliary where they bend over) appear to be subradially oriented. Accordingly all following lobes and lobules are sublongitudinally oriented.

The earlier adult suture lines were only observed on the two inner whorls of BGR, kv 145 beginning with the estimated shell diameter of 45 to 47 mm. The general shape and proportions of their elements are similar to those of more advanced adult sutures. However, they are considerably more shallowly and simply denticulated. Furthermore, the earliest visible sutures (compare Kemper 1978, Pl. 3, fig. 1) are either subradially oriented or slightly ascendant throughout. Though they have the same three auxiliaries from the very beginning, it is the first auxiliary instead of the second that is situated on the umbilical shoulder in the earliest visible sutures. It is followed by an especially wide fourth lateral saddle which is incomparably wider than that of the ultimate septate whorl. Already on the next, intermediate whorl the lateral part of the suture becomes distinctly ascendant and the umbilical part slightly descendant (though both less so than on the ultimate septate whorl). At the same time the first auxiliary lobe moves into its adult position on the lower flank while the second auxiliary moves to the outermost part of the umbilical wall (just below the umbilical shoulder). The further movement of these elements must have occurred on the now absent earliest one-third of the ultimate whorl.

The sculpture is even more variable than the shell shape. Typically developed bullae are present. They develop from the primary ribs rather early (at the latest at a shell diameter of 40 mm). The number of bullae per whorl varies between 16 and 22; it does not decrease noticeably in the adult. Furthermore, the adult bullae neither become stronger than the earlier bullae nor acquire a conical shape. Their comma-like bends result from the forward bend of their extensions on the umbilical wall. The strength of the bend varies from one specimen to another, from nonexistent (in a minority of specimens, e.g. BGR, kv 115 and BGR, kv 145) to strong (BGR, kv 117 or BGR, kv 118).

The ornament is relatively fine and dense. This is true, in particular, of the tertiary ribs on the venter. These ribs do not become weakened there even in the adult. The strength of the secondary ribs varies. Their course is only observable in a strong lateral light. The ornament commonly disappears on the addorsal halves of the whorls of adult specimens. The quasi-tridichotomous mode of bundling is prevalent but the points of subdivision are not situated at one level. This ribbing habit is especially characteristic of whorls with shell diameter of about 40 mm (BGR, kv 145).

Commonly, the ribbing becomes more complicated with increasing age. In these advanced stages only 2 secondary ribs arise out of each bullae in most instances. Other secondary ribs are simply intercalated. They begin in some instances at or above mid-flank. The number of supplementary ribs (i.e. secondary and tertiary) increases through a common branching of 2 to 4 tertiary ribs from a secondary rib. These tertiary ribs split off the secondaries at different levels. This mode of branching is particularly strongly expressed in the holotype where the branching points are situated rather adventrally. In other specimens these points are situated closer to mid-flank.

The course of ribs on the venter is variable. In some instances they cross it with more or less pronounced forward bends as do those of *Dichotomites*, while in others they are almost straight. This morphological feature is, therefore, not stable either.

Affinities and differences. The species evolved from the *Polyptychites multicostatus* stock, and is morphologically and phylogenetically intermediate between these *Polyptychites* and the more progressive *Prodichotomites* in all aspects of its morphology. The species differs from the ancestral *Polyptychites* forms in its more slender shell and a forward swing of ribs on the venter. It is connected by transitions with some of the late *Polyptychites* ex gr. *multicostatus* and with those *Prodichotomites* species which are directly derived from it. A taxonomic assignment of such morphologically intermediate forms may be difficult.

P. hollwedensis, which is diagnostic of the Lower/Upper Valanginian boundary beds, including the earliest late Valanginian of the Boreal Realm, presumably arose in the basins of Central and Northwest Europe and then migrated to the Arctic-Boreal and the Tethyan basins. A specimen from the Sverdrup Basin is described and figured as *P.* aff. *hollwedensis* in Chapter dealing with Canadian taxa. The ammonite from Southeast France figured by Thieuloy (1977, Pl. 8, figs. 2, 3) cannot be identified with a complete assurance because it is a juvenile. However, it most likely belongs to our species.

In spite of the more abundant material studied, the essentially *P. polytomus*-like adult external suture of *P. hollwedensis* is considerably less variable than that of the former, descendant species. Its material studied does not include any examples morphologically similar to the *Polyptychites hapkei*-like, extreme variant (e.g. BGR, kv 126; Figure 36a) of *P. polytomus* suture

Outside of the genus *Prodichotomites*, the adult external suture of *P. hollwedensis* is similar only to that of younger representatives of the *Polyptychites multicostatus* species group. The two are similar in all their taxonomically significant morphological features and appear to have similar ranges of their morphological variation. For example, the suture of the first variant of *P. hollwedensis* (Figures 38b 38c) resembles particularly closely those most complexly and deeply denticulated sutures of *Polyptychites orbitatus* that are characterized by adorally constricted lobes and relatively narrowed saddles (e.g. Koenen, 1902, Pl. IV, figs. 1, 3, 5). Conversely, the suture of its second variant (Figure 38a) resembles closely the less complexly denticulated sutures of *P. orbitatus*, which have relatively shorter and sturdier, parallel-sided lobes and wider saddles (e.g. Koenen, 1902, Pl. III, figs. 1, 3, 8; this paper Figure 32d). The sutures of *P. hollwedensis* and *P. orbitatus* cannot be reliably distinguished in the writers' opinion.

The equally similar terminal sutures of *Polyptychites saxonicus* (including *P.* aff. *saxonicus*; see Figures 26d, 32a) also appear to have a similar range of variation as and to be morphologically indistinguishable from those of *P. hollwedensis*.

The only known example of the adult external suture line of *Polyptychites tethyale* n. sp. (Figure 32c) also cannot be distinguished from that of the first extreme variant of the *P. hollwedensis* (compare Figures 38b, 38c).

These data fully support Kemper's (1978, p. 194, 195, Figure 3) conclusion that *P. hollwedensis* is a direct descendant of the *Polyptychites* ex gr. *multicostatus* based on other lines of evidence.

The adult external suture lines of *P. hollwedensis* are just as similar morphologically to the previously described, incompletely visible terminal sutures of the holotype of *P. polytomus* (Koenen, 1902, Pl. XLVI, fig. 4) and its representative designated as "*Polyptychites ramulosus*" by Koenen (1902, Pl. XLVI, fig. 1) in all their taxonomically significant morphological features. As already pointed out in the description of the *P. hollwedensis* sutures, these sutures of *P. polytomus* are similar respectively to the second and first extreme variants of the former. So far as they are known, these sutures of *P. polytomus* cannot be distinguished reliably from those of *P. hollwedensis*.

Prodichotomites pfaffi n. sp.

Pl. 15, fig. 1

Derivation of name. After the outstanding collector, the late Mr. E. Pfaff from Hildesheim, Lower Saxony.

Holotype. The original of Pl. 15, fig. 1 of this paper preserved in Hannover, BGR, kv 290.

Locus typicus. Twiehausen.

Stratum typicum. Lower/Upper Valanginian boundary beds, Hollwedensis-Zone.

Material. 5 specimens from Twiehausen, 4 of which are in private collections.

Diagnosis. A medium-sized species with a very broad umbilicus. Adult penultimate and ultimate whorls are low, broad and with broadly arched venter. Ribs are strongly prorsiradiately oriented.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
Holotype BGR, kv 290	129	45(35)	37(29)	48(37)	48	57

Description of the holotype. The oralmost whorl is occupied by the living chamber. The specimen is most probably adult so that its size comprises about 140 mm. The last whorl is wide and low. The venter is broadly arched at the beginning of the last whorl where its shape approximates that of a Roman arch. Then it becomes somewhat more narrow to the end of the shell. The shape of preceding whorls is unknown. However, these whorls are inferred to be more narrow and to have cross-sections proportioned like those of *P. hollwedensis*. The umbilical shoulder is broadly rounded. The umbilical wall is slightly convex and only moderately steeply oriented. The umbilicus measures 35 per cent and so is extraordinarily wide for the genus. It is step-like and only moderately deep.

The number of bullae on the penultimate whorl can only be estimated at 19. They are rather coarse as compared with those of other *Prodichotomites* species. The bullae become more refined and more numerous (20) on the earlier part of the last whorl. Only on its last quarter do they become coarser and illdefined. The bullae only extend for a short distance onto the umbilical wall where they are still radially oriented on the penultimate whorl. These extensions bend forward on the last whorl so that the bullae there acquire comma-like bends.

The suture line was not observed.

The strongly prorsiradiate and moderately strong sculpture is only visible on the last whorl. On the earliest part of this whorl each of the bullae produces 3 secondary ribs which bifurcate at different levels of the flank. This bundling habit is therefore quasi-tridichotomous. In the next growth stage one of the secondaries does not bifurcate. Then even this solitary secondary rib disappears, which results in the sculpture being reduced to irregularly bidichotomous bundles. Finally, the sculpture becomes weakened on the flanks.

Judging by very poor fragments of other specimens, the sculpture of the early growth stages is probably very fine and dense.

Affinities and differences. The species is a derivative of *P. hollwedensis* from which it differs, first of all, in a considerably wider umbilicus and a low, tubular cross-section of penultimate and ultimate whorls. It cannot be confused with any other *Prodichotomites*-species. The species was so far only found in the Lower Saxony Basin.

Prodichotomites robustus n. sp.

Pl. 14, figs. 1, 2

Derivation of name. From the robustly nodose sculpture, especially in the circumumbilical zone.

Holotype. The original of Pl. 14, fig. 2 preserved in Hannover, BGR, kv 291.

Locus typicus. Hollwede.

Stratum typicum. Lower/upper Valanginian boundary beds, Hollwedensis-Zone.

Material. 4 specimens from Hollwede preserved in BGR collections, Hannover.

Diagnosis. A medium-sized species with a narrow umbilicus, relatively wide whorls and a small number of coarse bullae (about 12 per whorl). The ribs are bent forward in the middle of the flank and on the venter.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
Holotype BGR, kv 291	115	25(22)	39(34)	51(44)	44	54
BGR, kv 292	114	31(27)	39(34)	44(39)	—	48?
BGR, kv 293	127	32(25)	42(36)	52(45)	49	61

Description. The species is only represented by adult whorls. However, these exhibit such remarkable and unique morphological characters that the erection of a new taxon is not only possible but necessary. The shell diameter measures approximately 130 mm. The whorls are moderately high and relatively wide. They are always wider than high. The greatest width of the whorls is situated in the zone of the umbilical shoulder. The flanks are moderately convex and meet in a relatively narrowly rounded ventral region. The umbilical shoulder is rounded. The relatively low umbilical wall is oriented relatively steeply on the penultimate whorl. However, it becomes more obliquely oriented on the living chamber. The width of the umbilicus comprises 22 to 25 per cent and so is very small for the genus. The specimen BGR, kv 292 (Pl. 14, fig. 1) must be interpreted as a widely umbilicate extreme variant, which connects the species with *P. hollwedensis*. The living chamber is at least one whorl long.

It was not possible to observe the suture line.

The bullae are typically developed and coarse for the genus. Their number per whorl is remarkably small. In the holotype it can be estimated at 13 while specimen BGR, kv 293 has 12. In the holotype the extensions of the bullae peter out in the outer third of the umbilical wall. However, in BGR, kv 293 they form rounded elevations which extend almost to the umbilical seam. They are oriented approximately radially to the beginning of the last whorl. However, they turn forward soon thereafter so that the oralmost bullae acquire a comma-like bend. On the adapical half of the last whorl of the holotype bullae split into 3 unequally strong secondary ribs, each of which splits into 2 tertiary ribs in a rather adventral position. The bundling habit becomes more irregular and the number of secondary and tertiary ribs decreases on the oral half of the last whorl. The ornament of BGR, kv 293 is already more irregular on the adapical half of the last whorl. The strength of secondary ribs in any one bundle is very unequal in all specimens studied. This phenomenon is particularly well expressed in the somewhat more finely ribbed specimen BGR, kv 292 (Pl. 14, fig. 2). In some instances only one of the secondary ribs is firmly attached to the bulla. The points of bifurcation of the secondary ribs are situated rather adventrally in all specimens studied. In addition to the above peculiarities, the incurved course of the ribs is also diagnostic. They bend forward in the middle of the flanks and also form a forward bend characteristic of *Prodichotomites* on the rounded venter.

Affinities and distinctions. The species has undoubtedly evolved from *P. hollwedensis* Kemper. It is known only from northwest Germany. The combination of the above-mentioned distinctive features is so typical that a confusion with other species is impossible. *P. robustus* n. sp. occurs in the Lower/upper Valanginian boundary beds.

Prodichotomites flexicosta (Koenen 1902)

Pl. 16, fig. 2; Pl. 17, figs. 1, 2; Pl. 18, fig. 1; Pl. 22, fig. 2;
Figures 39, 40a, 40b

*1902	*Craspedites flexicosta* Koenen, p. 74-76, Pl. 5, figs. 14-16.
1902	*Polyptychites gradatus* Koenen, p. 84, 85, Pl. 4, figs. 9-11.
1906	*Olcostephanus* (*Polyptychites*) *bidichotomus* Danford, Pl. 10, figs. 1, 1a.
1924	*Neocraspedites speetonensis* (for *O.* (*P.*) *bidichotomus* Danford 1906) Spath, p. 75.
?1969	*Dichotomites (Polyptychites) cf. petschorensis* Witkowski, Pl. 22, fig. 1.
1973	*Neocraspedites flexicosta* Kemper, p. 336, Table 1.
1977	*Prodichotomites* cf. *collignoni* Thieuloy, p. 415, Pl. 6, figs. 17-21.
1977	*Dichotomites* (*"Neocraspedites"*) *cf. flexicosta* Thieuloy, p. 421, Pl. 8, figs. 5, 6.
?1977	*Dichotomites* (*"Neocraspedites"*) sp. indet. A Thieuloy, p. 422, Pl. 8, figs. 11, 12.
1978	*Dichotomites* (*Prodichotomites*) *flexicosta* Kemper, Ernst and Thiermann, p. 20, Pl. 1, fig. 1.
1978	*Dichotomites* (*Prodichotomites*) *flexicosta-gradatus*-Gruppe Kemper, p. 218.

Holotype. The original of Koenen's (1902) Pl. 5, figs. 14-16 preserved in collections of the GIG Cat. No. 19.

Locus typicus. Hoheneggelsen.

Stratum typicum. Not definitely established, but most likely the latest lower to the basal upper Valanginian (Hollwedensis Zone).

Material. 16 specimens from Hollwede and Twiehausen in the BGR collections, Hannover.

Diagnosis. A medium-sized species with an umbilicus that is commonly narrow in early ontogenetic stages but becomes medium-sized later. The whorls are slender to moderately slender but their height decreases to average values in the late ontogenetic stages. Sculpture is fine and dense and becomes weakened to absent on the flanks of penultimate and ultimate whorls. The adult external suture line is essentially as in *Prodichotomites hollwedensis*, except for being straight and subradially oriented throughout.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
BGR, kv 121	156	40(26)	51(33)	65(42)	45	—
BGR, kv 122	130	32(25)	45(35)	54(42)	41	51
BGR, kv 123	92	17(19)	32(35)	43(47)	—	—
BGR, kv 296	111	23(21)	37(33)	52(47)	32?	43?

Description. The species is rather variable in all its morphological features. The holotype described and figured by Koenen (1902, Pl. 5, figs. 14-16) is septate throughout and only displays the appearance of intermediate growth stages. It belongs to those variants in which the flanks become smooth relatively early.

The material utilized in this paper includes several full-grown specimens. The maximum shell diameter reaches 170 mm. The length of the living chamber reaches one whorl.

Juvenile specimens have slender and (depending on their more or less progressive morphology) more or less high whorls (Pl. 16, fig. 2; Pl. 22, fig. 2). The whorls of progressive variants have subparallel flanks which are hardly convex. They become more strongly convergent and acquire a slight to moderate convexity in the later growth stages (Pl. 18, fig. 1B). This is particularly characteristic of the living chamber. The width of the whorl increases in late ontogeny. The venter is narrowly rounded and its shape varies according to the degree of convergence of the flanks (Figure 39). The umbilical shoulder is moderately rounded in the juvenile stages but becomes pronouncedly rounded in the three outermost whorls. On these three whorls it merges imperceptibly into a low, convex umbilical wall which is inclined at 70 degrees.

The umbilicus is shallow, pronouncedly step-like and more or less wide depending on the more or less progressive character and the ontogenetic stage of the specimens concerned. In the most primitive variants, which still approach *P. hollwedensis* Kemper, the umbilicus is wide throughout ontogeny. The development toward the very narrow umbilicate descendant — *P. complanatus* (Koenen) — followed a proterogenetic mode. Some specimens, as for example BGR, kv 123 (Pl. 17, fig. 1A) and BGR, kv 296 (Pl. 17, fig. 2A), are therefore narrowly umbilicate in juvenile growth stages (umbilicus of about 20 per cent) and wider (to 25 per cent) in the intermediate and adult growth stages. The timing of this widening depends on the degree of morphological progressivity of the specimens. In specimen BGR, kv 123 (Pl. 17, fig. 1) this change occurs at a shell diameter of about 90 mm.

Three good examples of adult external suture lines (i.e. those occurring on the last whorl before the adult living chamber) were studied. The specimens are BGR, kv 294, kv 328 (Figure 40a) and kv 349 (Figure 40b).

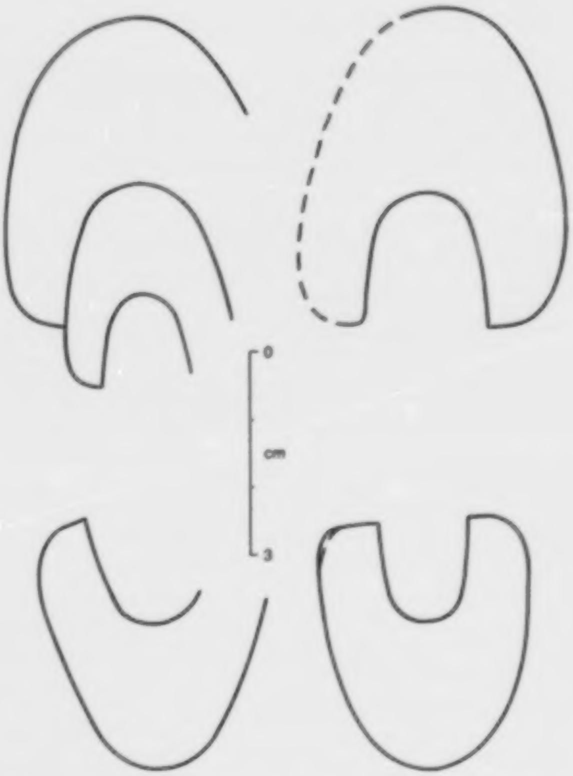


Figure 39. Cross-sections of two specimens of *P. flexicosta* (Koenen 1902). The vertical bar scale provides the magnification. Specimen BGR, kv 327 on the left is from Twiehausen clay pit while the specimen BGR, kv 328 on the right is from Hollwede clay pit.

These three sutures of *P. flexicosta* differ from those of *P. hollwedensis* and *P. polytomus* in being approximately straight and subradially oriented throughout. Judging by the drawings, the same is true of the adult suture line of the holotype of *P. flexicosta* (Koenen, 1902, Pl. V, figs. 14-16) and that of "*Polyptychites gradatus*" (Koenen, 1902, Pl. IV, figs. 9, 11) that is here synonymized with *P. flexicosta*. Furthermore, these personally studied sutures and that of the holotype (Koenen, 1902, Pl. V, figs. 14, 16) differ from those of *P. hollwedensis* and *P. polytomus* in their first lateral lobe being somewhat longer than the ventral lobe and about twice as long as the second lateral lobe.

All personally studied sutures are crowded with at least the tips of their two lateral lobes and the first auxiliary lobe touching and, sometimes, overlapping the tops of saddles of preceding sutures. The tips of their ventral lobes may or may not do so. However, their second and third auxiliary lobes always remain separated by at least some distance.

The shape and length of the lobes vary extremely strongly, stronger even than those of *P. hollwedensis*

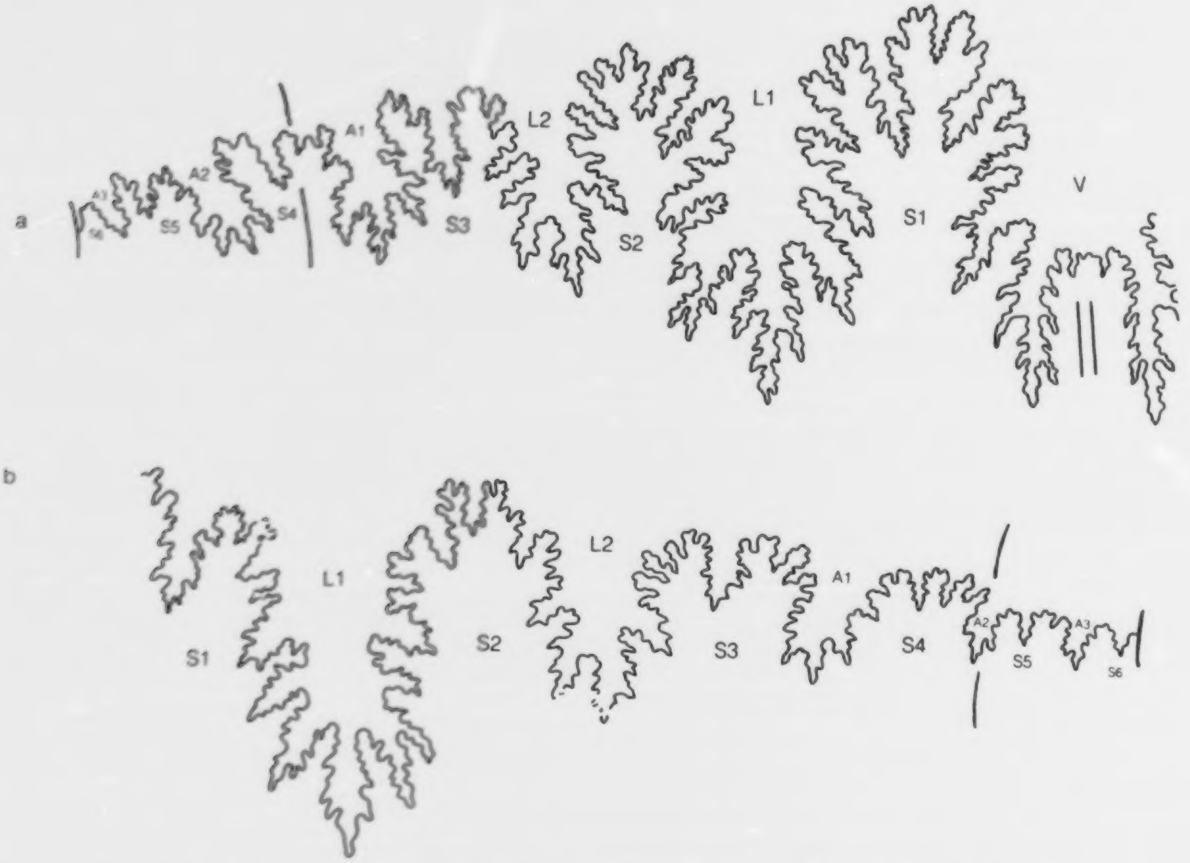


Figure 40. Adult external suture lines of *Prodichotomites flexicosta* (Koenen 1902). **a**. Specimen BGR, kv 328 at wh = 41 mm, x5.8 (approx.); **b**. Specimen BGR, kv 349 at wh = 46 mm, x5.4 approx. Both specimens are from Hollwede clay pit.

lobes. One extreme is represented by "*Polyptychites gradatus*" (Koenen, 1902, Pl. IV, figs. 9, 11) and the specimen BGR, kv 349 (Figure 40b). In these specimens all lobes, except for the first auxiliary in "*P. gradatus*", are wide, sturdy and taper markedly to slightly adapically. The width of their first and second lateral lobes is slightly more than one-half of their length. Their auxiliary lobes are similarly proportioned. The ventral lobe tapers adapically in "*P. gradatus*" but is parallel-sided in BGR, kv 349. The saddles of these specimens taper adorally in accordance with the adapical tapering of adjacent lobes and have either adorally convex or acute tops. The first and second lateral saddles are about as wide as the preceding lobes or only slightly wider. However, the third to fifth lateral saddles are considerably (up to three times) wider than the preceding lobes.

The two lateral lobes and the first auxiliary lobe are situated on the flank while the second auxiliary sits directly on the umbilical shoulder (Figure 40b). The third, and last, auxiliary lobe is situated within the inner half of the umbilical wall. The outer part of the sixth lateral saddle, that is about one and a half times wider than this auxiliary, separates it from the umbilical seam.

The here discussed extreme variant is characterized by the least complexly and most shallowly denticulated lobes and saddles (Figure 40b). The fairly long first order lobules of its ventral, lateral, and the first auxiliary lobes are, as a rule, devoid of the second order lobules and are only simply notched. The second auxiliary lobe either has short, simply notched first order lobules or is simply denticulated to notched. The third auxiliary lobe is always simply and shallowly denticulated. All lobules subdividing the first to fourth lateral saddles are either simply and shallowly denticulated or only notched. Those of the fifth and sixth saddles are either only notched or lack any kind of denticulation.

The other extreme, exemplified by the specimen BGR, kv 328 (Figure 40a), has relatively much more slender and long lobes, except for the second and third auxiliaries. For example, the first lateral lobe of BGR, kv 328 is 4 to 5 times longer than wide while the second lateral and the first auxiliary lobes are 4.5 to 5 times longer than wide. These lobes are markedly to distinctly constricted adorally and widened adapically.

The lateral lobes and the first auxiliary lobe of BGR, kv 328 are situated on the flank as in the other variant. However, the crest of the umbilical shoulder runs through the middle of the fourth lateral saddle. The second auxiliary lobe occupies the middle of the umbilical wall while the third auxiliary occurs in the middle of its inner third. It is separated from the umbilical seam by the outher half of the sixth lateral saddle.

Except for the third auxiliary, all lobes of BGR, kv 328 are considerably more complexly and deeply denticulated than those of the other extreme variant. Their principal lobules are mostly subdivided into shorter second order lobules which are either shallowly denticulated or simply notched. Even when the principal lobules are simply denticulated (e.g. in the second auxiliary), the denticles are relatively considerably longer and more slender. The tips of the lobules are either regularly rounded or at least somewhat rounded, contrary to the generally acute lobules of the other variant.

Though less slender (about three times longer than wide) the second auxiliary of BGR, kv 328 is considerably longer than that of the other variant. It is markedly constricted at the top and expands adapically. Only the third auxiliary has the same proportions as that of the other variant.

All lateral saddles of BGR, kv 328 are considerably more narrow than those of the other extreme variant (compare Figures 40a and 40b).

The adult external suture line of the specimen kv 294, and also that of the holotype of *P. flexicosta* (Koenen, 1902, Pl. V, figs. 14, 16), are morphologically transitional between those of the two above described extreme variants in every respect (e.g. shape, length, width, degree of denticulation, etc.).

Interestingly, the third auxiliary lobe of kv 294 is very broad and short, tapers adapically, is symmetrically trifid, and is otherwise not denticulated. It is considerably larger than those of kv 349 and 328 and is situated at the very umbilical seam. Hardly any part of the sixth lateral saddle is visible between it and the seam.

The sculpture is fine and dense. It is, furthermore, characterized by the flanks becoming smooth at least in the adult. The growth stage at which sculptural weakening begins varies strongly and depends, like that of the widening of the umbilicus, on the degree of progressivity of the specimens concerned. Bullae are typically developed and appear already early in the ontogeny (at shell diameters of 20 to 30 mm). They persist to the adult mouth border but become either weaker or somewhat wider and indistinctly limited on the living chamber. The bullae are sharp, comma-like structures on those whorls which precede the third before last whorl and in part on the later whorls. Their extensions peter out, as a rule, on the outer third of the umbilical wall. The primary ribs of the early whorls are not comma-like but are oriented radially. The number of bullae on the penultimate whorl varies between 16 and 20. This number does not decrease noticeably on the adult living chamber.

On the early whorls nearly all secondary ribs (3-4) branch off the bullae. However, on the penultimate whorl some of them are intercalated. They begin then at different levels on the flank. The splitting into tertiary ribs occurs rather high on the flank. The bundling habit is, therefore, irregular, all the more so as the individual tertiary ribs may also be intercalated. There are at least two and commonly even three tertiary ribs per secondary rib. Their subdivision points are situated at different levels. It is impossible to discern the bundling habit and the arrangement of ribs of the most complicated sculptural stage, which is situated on the penultimate whorl, as the flanks become smooth at that stage if not earlier. In the adult, a crown of adumbilical bullae is opposed by a crown of finer ribs on the ventral shoulder and venter (Pl. 17, fig. 2A). These bullae and ribs are more or less pronouncedly incurved forward. The strength of the ribs is variable.

Affinities and differences. The species evolved from *P. hollwedensis* via a proterogenetic narrowing of the umbilicus and an increase in whorl height combined with an increase in density of the sculpture. Another distinctive feature is an increasing weakening of the sculpture on the flanks, which follows a palingenetic mode. Finally, its generally *P. hollwedensis*-like suture line differs in being straight and subradially oriented throughout. There are transitional forms connecting *P. flexicosta* with the ancestral species, and also with the end member of the evolutionary lineage -- *P. complanatus* (Koenen). In the latter species the narrow umbilicus persists into the adult growth stage. This results in the development of a very narrowly umbilicate, very slender and almost smooth ammonite superficially similar to extreme representatives of *Neocraspedites*. *P. flexicosta* is morphologically and phylogenetically intermediate between *P. hollwedensis* and *P. complanatus*.

A confusion with other late Valanginian species of *Prodichotomites* is impossible because of the relatively wide umbilicus of *P. flexicosta*. *P. fissuratus* (Koenen) has a very different sculpture with thickened bullae and primary ribs.

P. flexicosta is a species which is important for the purpose of interregional correlations. In addition to the Lower Saxony Basin, it occurs in the North Sea Basin system (Speeton), in Poland (Witkowski, 1969) and even in Southeast France, in the Tethyan Realm (Thieuloy, 1977). Further details can be extracted from its synonymy.

The general similarity of *P. flexicosta* external suture to that of *P. hollwedensis* confirms Kemper's (1978, p. 194, 195, Figure 3) idea of its being a direct descendant of this species and, ultimately, of *Polyptychites* ex gr. *multicostatus* (Figure 11).

Prodichotomites complanatus (Koenen, 1902)

Pl. 15, fig. 2; Pl. 16, fig. 4; Pl. 20, figs. 3, 4; Figure 41a

*1902 *Craspedites complanatus* Koenen, p. 72, 73; Pl. 5, figs. 11-13; Pl. 6, figs.18, 19.

1969	*Craspedites complanatus* Witkowski, Pl. 19, fig. 5.
1973	*Neocraspedites complanatus* Kemper, p. 337, Table 1.
1976	*Dichotomites (Prodichotomites?)* sp. indet. Kemper, Pl. 28, fig. 3.
1976	*Dichotomites (Prodichotomites)* aff. *undulatus* Kemper, Pl. 31, fig. 16.
1977	*Prodichotomites collignoni* Thieuloy, p. 413-415, Pl. 6, figs. 12-16.

Lectotype. The original of Koenen's (1902) Pl. 5, figs. 11-13 is here selected as the lectotype. It is preserved in the collections of GIG, Cat. No. 451-3.

Locus typicus. Hoheneggelsen.

Stratum typicum. Lower/upper Valanginian boundary beds, most likely the upper, basal upper Valanginian part of the Hollwedensis-Zone.

Material. 13 specimens from Hoheneggelsen and Twiehausen.

Diagnosis. Medium-sized species with an exceptionally narrow umbilicus. Flanks are subparallel. They are devoid of sculpture already early in the ontogeny. So far as it is present, the sculpture is delicate and fine. All elements of the advanced adult suture line are strongly shortened and widened. Its lobes taper adapically while the saddles widen in that direction. Second and third order denticulation is extremely dense and refined.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
Lectotype	72	11(15)	26(36)	35(49)	15	25
BGR, kv 124	108	17(16)	42(39)	50(46)	—	—
BGR, kv 298	88	14(16)	35(40)	39(44)	25?	33
BGR, kv 299	113	21(18)	43(38)	49(43)	—	—
BGR, kv. 300	100	18(18)	36(36)	45(45)	—	—

Description. The figures of the lectotype in Koenen (1902) are fairly accurate. This is less applicable to the second figured specimen (Koenen, 1902, Pl. 6, figs. 18, 19), which cannot be placed in the species with total confidence. This specimen could represent a juvenile shell of an allied species such as *P. undulatus* (Koenen).

When evaluating the characteristic features of the species, one must consider that it is the last member of an evolutionary lineage, which starts with *P. hollwedensis* and has *P. flexicosta* as an intermediate member. Because of these relationships transitional forms to the preceding species exist. Furthermore, one has to distinguish between more or less progressive variants within each of these species. The lectotype and the large specimens of *P. complanatus* figured here (Pl. 15, fig. 2; Pl. 16, fig. 4) represent its extreme variants. Therefore they display its typical features most clearly and exhibit the *Neocraspedites*-like appearance particularly well. They are presumably the youngest members of the lineage while the forms which retain the sculpture through a greater part of the ontogeny should be considered as older and more primitive variants *(e.g. "Prodichotomites collignoni"* Thieuloy). As with all taxa described in this paper, we prefer to use a broad species concept for *P. complanatus*. This is the only practicable approach in view of its great variability and the presence of transitional forms connecting it with allied species.

The lectotype is septate to the end. The living chamber is not preserved in the majority of other studied specimens either. Only specimens BGR, kv 124 (Pl. 16, fig. 4) and BGR, kv 299 (not figured) are evidently adult and respectively almost complelely or completely preserved. The complete specimen BGR, kv 299 has a maximum shell diameter of 140 mm and shows that the living chamber of this species (like that of others) occupies one complete whorl. The whorls are very slender and high. The flanks are only very insignificantly convex. Their course fluctuates between subparallel and moderately convergent. The venter is narrow. It is low and obtusely rounded at least in the intermediate growth stages. The flanks merge into a low and feebly to pronouncedly convex umbilical wall across a rounded umbilical shoulder.

The umbilicus is very narrow (about 16 percent) in the young and intermediate growth stages but then widens to about 18 percent in the adult. Because of a strong involution and the convexity of the umbilical wall, the umbilicus is funnel-like initially. However, because of increasing evolution in the penultimate and ultimate whorls, it becomes step-like in the adult.

The advanced adult external suture line was studied in the specimens BGR, kv 124 (Pl. 16, fig. 4; Figure 41a) and BGR, kv 299 (unfigured). Earlier adult sutures were studied in the figures of the lectotype (Koenen, 1902, p. 72, 73; Pl. V, figs.12, 13) and in the specimen BGR, kv 298 (Pl. 15, fig. 2).

The two advanced adult sutures, which are similar in all essential details, differ strongly from all other presently known *Prodichotomites* sutures, including the earlier adult sutures of *P. complanatus*. As exemplified by the specimen BGR, kv 124 (Figure 41a), all its uniquely short and sturdy lobes are either twice as long as they are wide or shorter. The auxiliaries are especially sturdy, their length and width being commonly subequal. All lobes taper strongly adapically. Their first order terminal and lateral lobules are also shortened while being at the same time (uniquely for the genus) closely and finely ornamented by the second order lobules and notches. These finer denticulations are invariably sharp-tipped. This ornamentation of the first order lobules is so delicate that it was impossible to draw all of its details in the Figure 41a. These fine and finest details are much better visible in the photograph of the specimen BGR, kv 124 (Pl. 16, fig. 4). The second and third auxiliaries either lack these second order lobules and notches or exhibit but very little of them. However, even these lobes are

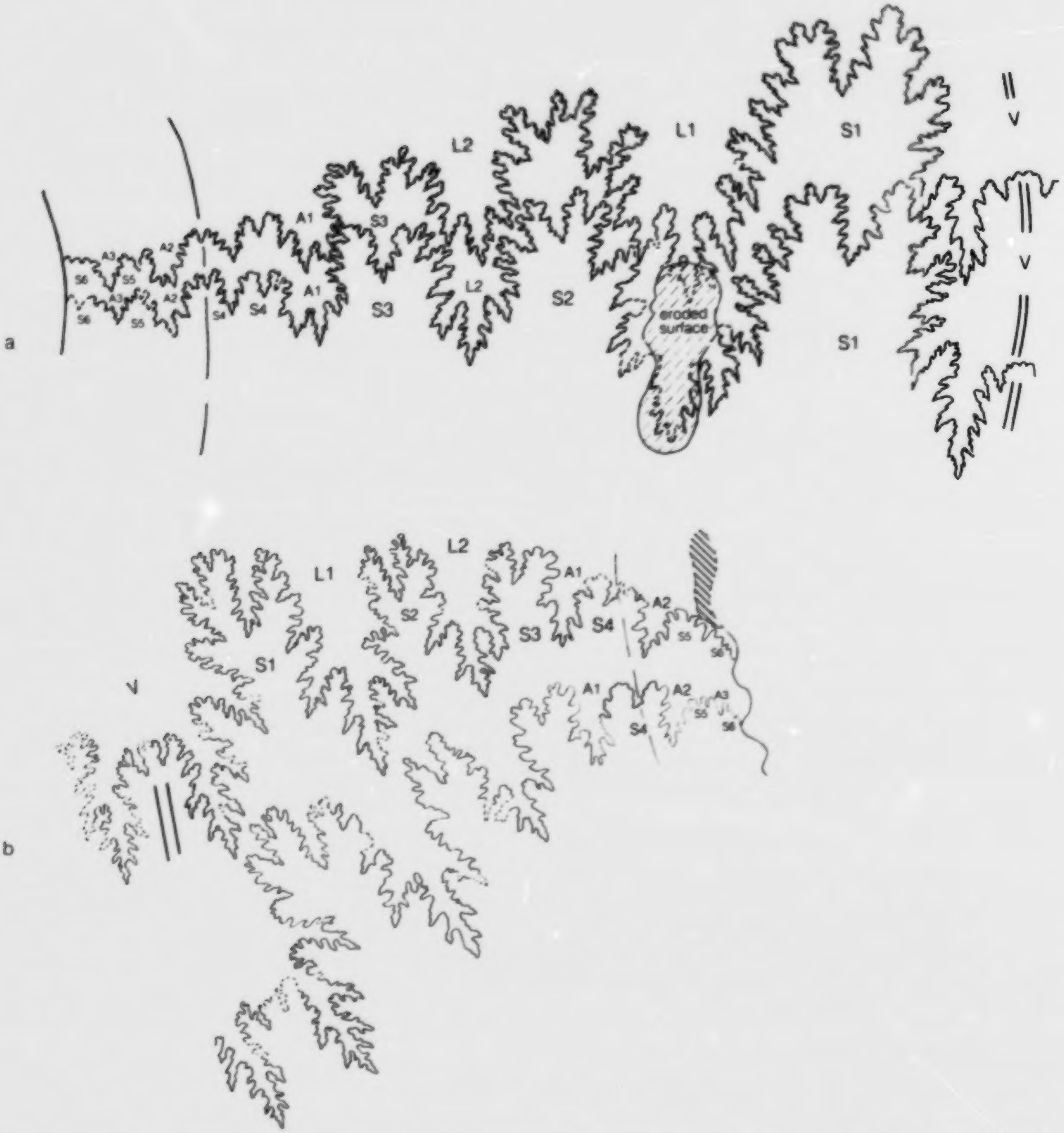


Figure 41. **a.** Adult (oralmost) external suture lines of *Prodichotomites complanatus* (Koenen) at the whorl diameter of 102 mm, x2.7 (approx.). BGR, kv 124. **b.** Adult external suture lines of *Prodichotomites glaber* n. sp. at the whorl diameter of 55 mm, x1.8 (approx.). BGR, kv 144.

more finely and closely denticulated than their equivalents in other *Prodichotomites* species.

The lateral saddles are shortened, sturdy and taper adorally proportionally to the adjacent lobes. Their sturdy and relatively short first order lobules are again similar to those of the adjacent lobes and mostly (e.g. except for the fifth and sixth lateral saddles) ornamented by similarly refined and closely spaced second order lobules and notches. The considerably coarser and sparser denticulated fifth and sixth lateral saddles are again relatively more finely and closely denticulated than their equivalents in other *Prodichotomites* species.

All external sutures observed in BGR, kv 124, (Pl. 16, fig . 4) and BGR, kv 299 are strongly crowded. The tips of most lobes (except for those of the second and third auxiliaries) touch and, sometimes, overlap the tops of the saddles of preceding sutures, which makes it difficult to draw them accurately.

The earlier adult external suture of the holotype (Koenen, 1902, p. 72, 73; Pl. 4, figs. 12, 13) resembles the advanced to terminal adult sutures of the BGR, kv 124 and BGR, kv 299 in part only. Only its ventral lobe, the two lateral lobes, the first auxiliary lobe, as well as the first and second lateral saddles, are shaped, proportioned and denticulated like their equivalents in the latter sutures. Furthermore, the degree of their shortening, widening and adapical tapering (or adapical widening of the saddles) are distinctly to much less marked than those of their equivalents in the sutures of BGR, kv 124 and BGR, kv 299. This is most evident in their terminal lobules and in the only slightly shortened and adapically tapering first auxiliary. The third to sixth lateral saddles, the second and third auxiliary lobes, and all their lobules and notches are unlike their equivalents in the sutures of BGR, kv 124 and BGR, kv 299. Instead, they resemble the equivalent elements of more complexly built suture variants of *P. flexicosta* (Figure 40a) and *P. hollwedensis* (Figure 38b).

The earlier adult external suture of BGR, kv 298 (Pl. 15, fig. 2A) differs even stronger from the advanced adult sutures of BGR, kv 124 and BGR, kv 299. Even the first and second lateral lobes of this suture are slender, long, and subparallel-flanked. Its first and second lateral saddles do not exhibit any sign of adapical widening. These lobes and saddles, and all other lobes and saddles of this suture, are shaped, proportioned, and denticulated much like their equivalents in *P. flexicosta* and *P. hollwedensis*.

This restriction of the uniquely aberrant morphology of adult external suture of *P. complanatus* to some oralmost three-quarter whorl of its phragmocone could hardly be either a pathological phenomenon or an individual aberration as it is developed entirely similarly and equally strongly in both adults studied. Furthermore, the earlier adult suture of the holotype exhibits the same aberrant morphology, albeit in a less extreme and more localized form. Finally, this morphology recurrs, again in a less extreme and more localized form, in the less advanced adult external suture of the holotype of *P. fissuratus* (Koenen, 1902, Pl. V, figs. 1, 2), which is the closest known ally of *P. complanatus*. This aberrant morphology is interpreted accordingly as a pronounced, presumably adaptive specialization of the advanced adult suture of *P. complanatus*. This explanation agrees well with this species being apparently the terminal member of the *hollwedensis-flexicosta-complanatus* lineage that died out without issue (Kemper, 1978, Figure 3; this paper Figure 11).

The advanced external suture of *P. complanatus* resembles morphologically some advanced sutures of *Polyptychites* ex gr. *pavlowi-keyserlingi* combining the sturdy, adapically tapering lobes with the presence of three auxiliary lobes (e.g. Pl. 7, fig. 1; Figures 25a, 25c). However, the above described ontogeny of this suture in combination with the phylogeny and stratigraphy of *P. complanatus* reveals the purely homeomorphic character of this similarity.

The adult external suture of *P. complanatus* is somewhat ascendant (some 5 to 10 degrees) on the flank where it is approximately straight. Then it abruptly becomes distinctly descendant over the first auxiliary and continues on that course to the umbilical seam (Pl. 16, fig. 4; Figure 41a). The umbilical seam either cuts through the partly exposed sixth lateral saddle, or even coincides with the sometimes partly exposed fourth auxiliary lobe.

The character of the sculpture varies depending on the growth stage and the degree of progressivity of specimens concerned. Furthermore, it is necessary to distinguish between very delicately and only moderately finely ribbed variants. The bullae develop gradually from delicate or thickened primary ribs. They are so low and slight in all growth stages that it is only possible to recognize them with the aid of a lateral light. They are comma-like and number about 16 on the penultimate and ultimate whorls.

The juvenile specimens figured in Kemper (1976, Pl. 28, fig. 3 and Pl. 31, fig. 16) and reproduced here in Pl. 20, figs. 3, 4, belong to especially finely ribbed variants. The majority of specimens have somewhat coarser ribs, although the sculpture remains always delicate and dense. Because the decline of sculpture on the flanks begins early, it is only possible to observe the bundling habit in the early growth stages. The secondary ribs are commonly only indistinctly attached to the primary ribs, which results in an only apparent bundling of ribs. These bundles are, however, not fasciculate as they include tertiary ribs which arise either by a dichotomous splitting up of a secondary rib or by an intercalation on the more adventral parts of the flanks. The length of the primary rib, which later transforms into a bulla, is variable. The specimen figured by Koenen (1902, Pl. 6, figs. 18a, 18b) develops long and somewhat swollen structures which subdivide in two in the mid-flank zone and then transform into tertiary ribs higher on the flank. Details of the arrangement of secondary and tertiary ribs are provided by specimens reproduced in Pl. 20, figs. 3, 4.

German localities that have yielded representatives of our species (especially Twiehausen) are situated particularly in the upper part of the Hollwedensis-Zone. There are prevalent accordingly the progressive variants, in which the sculpture on the flanks is lost very early. Commonly this process began by a shell diameter of 20 mm and, at any rate, not later than at a diameter of 40 mm. In these growth stages the sculpture consists of a crown of feeble bullae which is opposed by a crown of finer ribs on the ventral shoulder and venter (Pl. 15, fig. 2A; Pl. 16, fig. 4). The juvenile shells described by Thieuloy (1977, Pl. 6, figs. 12-16) as *Prodichotomites collignoni* are considered to be less progressive variants derived from older beds. They are morphologically and phylogenetically transitional to *P. flexicosta*. The reduction of sculpture begins later in these variants. The specimens described as *P.* cf. *collignoni* by Thieuloy (1977, Pl. 6, figs. 17-21) are even more pronouncedly primitive. They are placed in *P. flexicosta* in this paper.

Affinities and differences. Neocraspedites-like homoeomorphs exist in other late Valanginian *Prodichotomites*-

lineages. In *P. undulatus* the secondary ribs on the flanks persist instead of being reduced. *P. glaber* is considerably larger and thicker. It also differs in the presence of a coarser sculpture in the proximity of the umbilical shoulder and on the venter. *P. complanatus* differs from the still younger homoeomorphs of *Neocraspedites* (e.g. *P. perovalis*, *P. ivanovi*) in its smaller size, more obtusely rounded venter, and narrower umbilicus which widens irregularly in advanced ontogenetic stages. The sculpture of *P. complanatus* is finer, denser, less pronounced and more strongly reduced on the flanks. Finally, its advanced adult external suture line has uniquely sturdy and short, adapically tapering lobes.

P. complanatus has a wide geographic range and is accordingly a very important species for the purpose of interregional correlations. Outside the Lower Saxony Basin, it has been found in Poland and Southeast France. Its real geographic range should have been considerably more extended than that.

Prodichotomites fissuratus (Koenen, 1902)

*1902	*Craspedites fissuratus* Koenen, p. 78-80, Pl. 5, figs. 1, 2 (figs. 3, 4?).
non 1977	*Dichotomites* ("*Neocraspedites*") cf. *fissuratus* Thieuloy, p. 420, Pl. 8, figs. 2, 3.

Lectotype. The original to Koenen's (1902), Pl. 5, figs. 1, 2 is here selected as the lectotype of *P. fissuratus*. It is preserved in collections of the GIG, Cat. 451-1.

Locus typicus. Hoheneggelsen.

Stratum typicum. Probably lower/upper Valanginian boundary beds, most likely upper part of Hollwedensis-Zone.

Material. Only the lectotype.

Diagnosis. The whorls are slender but low. The umbilicus is moderately narrow. Bullae and secondary ribs have an irregularly knot-like appearance. Tertiary ribs fine and dense. Adult external suture line is specialized like that of *P. complanatus* but considerably less strongly.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
Lectotype	79	17(22)	27(34)	35(44)	—	—

Discussion. This rare and poorly understood species is interesting largely because the earlier external suture of its wholly septate lectotype (? the second penultimate whorl) is specialized somewhat like that of the holotype of *P. complanatus* (compare Koenen, 1902; Pl. V, figs. 12, 13). This similarity is expressed in a marked shortening and apical tapering of the ventral and first lateral lobes and an equally marked apical widening of the first and second lateral saddles. However, already the second lateral lobe is slender, parallel-flanked and generally similar to that of *P. flexicosta* and *P. hollwedensis*. Furthermore, the same is true of all other lobes and saddles. The advanced adult suture line of *P. fissuratus* is not known. It may possibly be even more similar to that of *P. complanatus* than are their earlier adult sutures.

The sutural morphology of *P. fissuratus* indicates that it is a close ally (?perhaps a morphologically extreme variant) of *P. complanatus* and another terminal member of the *P. hollwedensis — P. flexicosta — P. complanatus* lineage, as was already proposed by Kemper (1978, p. 194, 195, Figure 3). *P. fissuratus* is only a homoeomorph of *P. undulatus* because the adult external suture line of the latter is very different and similar to that of *P. ivanovi* (e.g. Figure 41b).

The reader is referred to the description provided by Koenen (1902, p. 78-80) for other aspects of the morphology of *P. fissuratus* as no additional material has been found. Further discussion of this species is provided in the description of *P. undulatus* (Koenen).

Prodichotomites undulatus (Koenen 1902)

*1902	*Craspedites undulatus* Koenen, p. 70-78, Pl. 5, figs. 5-7).

Holotype. The original of Koenen's (1902) Pl. 5, figs. 5-7 preserved in the collections of the GIG, Cat. No. 451-2.

Locus typicus. Hoheneggelsen.

Stratum typicum. Lower/upper Valanginian boundary beds, most likely the upper, basal Valanginian part of the Hollwedensis Zone.

Material. In addition to the holotype, two more incompletely and poorly preserved specimens. One of them is from Hoheneggelsen while the other is from Hollwede.

Diagnosis. Very narrowly umbilicate and slender species. Sculpture on the venter is fine and dense. The secondary and tertiary ribs are clearly differentiated. The secondary ribs on the flanks do not disappear. The adult external suture line similar to the most complexly denticulated and most slender lobed variant of the *P. flexicosta* and *P. hollwedensis* suture line.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
Holotype	80	12(15)	30(38)	38(47)	21	31

Discussion. The reader is referred to the description of the species provided by Koenen (1902) for most aspects of its morphology as no significant supplementary material has been found subsequently. However, the hitherto neglected morphology of the adult external suture line indicates clearly that it is only indirectly related to the *Prodichotomites complanatus-fissuratus* species group. Koenen's (1902, Pl. 4, figs. 6, 7) reproduction of this suture indicates a complete absence of the specialization characteristic of that of *P. complanatus* and *P. fissuratus*. Instead this suture line has very long, slender and richly denticulated lobes similar to the most complex and slender examples of *P. hollwedensis* (e.g. Figure 38b, 38c) and *P. flexicosta* (e.g. Figure 40a) lobes. Furthermore, this suture has narrow saddles that are deeply penetrated by long and slender, richly denticulated lobules of the flanking lobes. This is true even of the third and fourth lateral saddles. These saddles are appreciably more narrow and more deeply denticulated than the most narrow and deeply denticulated saddles known in *P. hollwedensis* and *P. flexicosta*. They compare closely only with those of *P. ivanovi* (e.g. Figure 41b) in these respects.

Like all other adult sutures of the *P. hollwedensis-P. flexicosta-P. complanatus* lineage, that of the holotype of *P. undulatus* actually exhibits three well developed auxiliary lobes (the third auxiliary is not visible in Koenen's drawing) between the second lateral lobe and the umbilical seam. This seam either runs through some part of the sixth lateral saddle or occurs already at the beginning of the fourth auxiliary lobe.

Because of the character of its adult suture line, *P. undulatus* is here considered to be an independent offshoot of *P. hollwedensis* that evolved in a different direction than the lineage leading from *P. hollwedensis* toward *P. flexicosta* and then to *P. complanatus* (and *P. fissuratus*).

The combination of a still rather wide umbilicus with the already slender, discoidal whorl shape characteristic of *P. undulatus* is assumed to be a feature independently derived from *P. hollwedensis* instead of one indicating a direct derivation from *P. fissuratus*. The same would also apply to the possibly present (only inferred tentatively because of a poor preservation of all material available) umbilical widening in the adult.

Other than in its suture line, *P. undulatus* differs from the otherwise similar *P. flexicosta-P. complanatus* lineage especially in its sculpture. The bullae are strongly and typically developed. They give rise to pronounced, or at least clearly expressed, secondary ribs which, so far as it is possible to recognize in the material available, do not become weakened on the flanks. The secondary ribs follow an irregular course and are predominatly bundled in the bullae. The tertiary ribs split off them rather high on the flanks. Their number per bundle is high (about 8). They arise only relatively rarely by bifurcation of secondaries as the majority are intercalated.

Prodichotomites glaber n. sp.

Pl. 19, fig. 1; Pl. 20, fig. 2; Pl. 21, fig. 1;
Pl. 22, fig. 1; Figures 41b, 42a, 42b.

1929 *Polyptychites perovalis* Frebold, p. 8, Pl. 1, fig. 1.

1929 *Polyptychites cf. perovalis* Frebold, p. 8, 9, Pl. 3, fig. 1

1972 *Subcraspedites* (*Borealites*) *freboldi* (Shulgina and Yershova n. sp.). Shulgina in Saks et al., p. 123 (a nomen nudum).

Origin of name. After the flanks which are smooth in adult growth stage. Glaber (lat.) means smooth.

Holotype. The original of Pl. 22, fig. 1 of this paper preserved in Hannover, BGR, kv 305.

Locus typicus. Hollwede.

Stratum typicum. Not known exactly, apparently the lower/upper Valanginian boundary beds of the Hollwedensis Zone.

Material. 4 specimens from Hollwede, 1 indifferently preserved and fragmentary (last whorl or its fragments) specimen from Twiehausen, 1 fragment from Hasslage-Nord and 2 specimens from Spitsbergen.

Diagnosis. A large species with relatively thick whorls and a narrow umbilicus. The sculpture is only moderately fine and is characterized by a distinct decrease of the number of bullae in the adulthood. The penultimate and ultimate whorls have a *Neocraspedites*-like appearance because of a weakening of the sculpture on the flanks. Adult external suture line similar to the less complexly and less deeply denticulated variants of the *P. hollwedensis* and *P. polytomus* sutures, except that its umbilical part (beginning with the first auxiliary lobe) is considerably more strongly retractive and that its lobes and lobules are considerably smaller, sturdier and less denticulated to simple.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
Holotype BGR, kv 305	111	25(23)	38(34)	48(43)	33	45
BGR, kv 303	158	32(20)	58(37)	68(43)	48	57
BGR, kv 306	146	33(23)	51(35)	62(43)	—	—

Description. The species is large. The largest German specimen (BGR, kv 303; Pl. 21, fig. 1) has a shell diameter of 190 mm whilst a specimen from Spitsbergen (Frebold, 1929, Pl. 3, fig. 1; plaster cast in BGR collections under No. kv 304) has one of at least 230 mm. The living chamber occupies all of the last whorl.

The holotype is only slightly progressive morphologically and resembles still the ancestral species *P. polytomus* (Koenen). Therefore it still has relatively more numerous bullae. The fragment figured in Pl. 20, figs. 2A, 2B (BGR, kv 302) affords a better idea of some of the typical morphological features of the species. It is narrowly umbilicate, relatively thick and has a rather obtusely rounded venter. The shape of this venter is aberrant as it is narrowly arched as a rule. Specimen BGR, kv 302 has only feebly convex, distinctly adventrally converging flanks which are already devoid of sculpture in the middle parts.

The last whorl of the holotype is a living chamber, which is most likely not an adult chamber. This whorl is relatively slender. The flanks are only feebly convex and at the same time distinctly convergent adventrally. The venter is narrowly rounded. The greatest width of the whorls is situated in the proximity of the umbilical shoulder. The latter is pronouncedly rounded and merges into a low and convex umbilical wall. Because of these properties and a strong involution (about 87 per cent), the narrow umbilicus (23 per cent) is funnel-like. The umbilicus is furthermore similarly developed throughout the ontogeny as it either does not exhibit any widening or only widens slightly.

The holotype does not exhibit the suture line. However, it is visible in specimens BGR, kv 144, BGR, kv 302, BGR, kv 303. The complete and well preserved earlier adult external suture of BGR, kv 144 (Pl. 19, fig. 1; Figure 41b), that represents a form morphologically transitional between *P. polytomus* and *P. glaber*, is the best example known. Judging by it and the less completely and less well preserved terminal adult sutures of BGR, kv 302 (Pl. 20, fig. 1A) and BGR, kv 303 (Pl. 21, fig. 1A), the adult external suture of *P. glaber* is similar to the less slender and less complexly and deeply denticulated variants of the sutures of *P. hollwedensis* (Figure 38a) and *P. polytomus* (e.g. that of its holotype figured by Koenen, 1902, Pl. XLVI, fig. 4) in most of its taxonomically significant features. Its umbilical part beginning with the first auxiliary lobe appears to be considerably stronger and at that increasingly descendant (Pl. 19, fig. 1A; Figure 41b) than that of the other two species. Furthermore, its umbilical lobes and lobules (again beginning with the first auxiliary lobe) are considerably smaller, sturdier and less denticulated to simple. The umbilical seam cuts through the third auxiliary lobe in BGR, kv 302, and BGR, kv 303 but it cuts through the middle part of the next following sixth lateral saddle in BGR, kv 144 (Figure 41b). The taxonomic value of all these distinctions is uncertain.

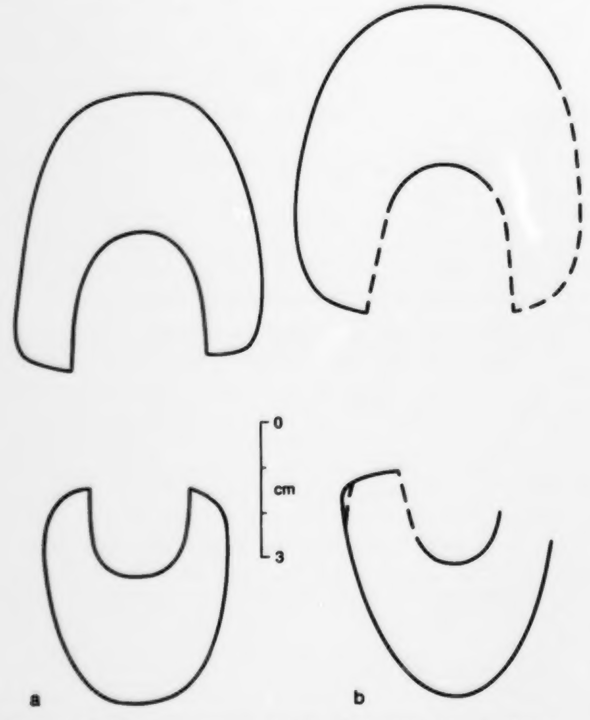


Figure 42. Cross-sections of *Prodichotomites glaber* n. sp. **a**. Specimen BGR, kv 302. **b**. Specimen BGR, kv 329. A transitional form between *Prodichotomites polytomus* and *P. glaber*. Both specimens are from the Hollwede clay pit, Northwest Germany. Upper Valanginian. The magnification is provided by linear scale.

The last preserved whorl of the holotype is ornamented by 18 bullae as compared with 22 on the penultimate whorl. As attested by other specimens, this trend towards a decrease in the number of bullae throughout ontogeny is very typical for the species. It is maintained to adulthood. In specimen BGR, kv 303 (Pl. 21, fig. 1A) the number of bullae on the adult last whorl decreases to 16. In BGR, kv 302 (Pl. 20, fig. 2) the number is estimated to be even smaller. The adult bullae are also weaker than the earlier bullae. As visible in the holotype, the bullae of the preceding whorls are strongly expressed and typically developed. On the last two whorls of the holotype the bullae are strongly comma-like. Their extensions on the umbilical wall peter out between its middle and outer thirds. The primary elements of the preceding whorls are oriented radially. However, they are here expressed as ribs rather than bullae.

At the beginning of the last preserved whorl of the holotype two unequally strong secondary ribs issue from every bulla (Pl. 22, figs. 1A, 1C). These secondaries bifurcate at different levels on the outer half of the flank. Additional tertiary ribs occur between the bifurcations of tertiary ribs. Additional secondary ribs may also be present on occasion. The ribbing habit is very irregular because of different levels of starting points of tertiary ribs and an unequal strength of secondary ribs.

On the last three-quarters of the whorl of the holotype the ornament of the flanks is already too strongly weakened to permit any observation of the mode of bundling. The adult ornamentation consists of weak, pronouncedly comma-like bullae, which are few in number, and a crown of moderately fine supplementary ribs on the ventral shoulders and venter. The ribs are variably strongly inclined forward in that zone. The adult sculpture acquires a strong forward bend on the outer halves of the whorls.

The two Spitsbergen representatives of the species (Frebold, 1929, Pl. 1, figs. 1a, 1b; Pl. 3, fig. 1) agree well with its NW German representatives. They only differ in being considerably larger. The shell diameter of the second specimen (Frebold, 1929, Pl. 3, fig. 1) can be estimated at about 240 mm. The species therefore follows the general trend of the Arctic Polyptychitinae toward an increased size.

Affinities and differences. P. glaber developed from *P. polytomus* (Koenen) via an increase of the whorl height, as well as an increase of the involution and the shell size. Furthermore, it is characterized by a weakening of the sculpture on the flanks of the last two whorls and a decrease of the number of bullae in the course of the ontogeny. It is not possible to confuse *P. glaber* with other early *Prodichotomites* species which have a *Neocraspedites*-like appearance (e.g. *P. complanatus*, *P. undulatus*), because of its much larger shell size and thicker whorls.

The species of the principal evolutionary lineage of *Prodichotomites* (*P. perovalis* and *P. ivanovi*) are still more narrowly umbilicate, have considerably more slender and adventrally very narrowly rounded whorls and a denser sculpture with more delicate bullae.

P. glaber is known from Northwest Germany and Spitsbergen.

Prodichotomites perovalis (Koenen 1902)

Pl. 23, figs. 1, 2; Figures 43, 44a, 44b.

1884	*Ammonites (Olcostephanus)* cf. *Grotriani* Weerth, p. 17, Pl. 3, figs. 4a, 4b.
*1902	*Polyptychites perovalis* Koenen, p. 87, 88; Pl. 47, figs. 3, 4.
non 1929	*Polyptychites perovalis* Frebold, p. 8; Pl. 1, figs. 1a, 1b.
non 1929	*Polyptychites* cf. *perovalis* Frebold, p. 8, 9, Pl. 3, fig. 1.
1937	"schwach gerippte Craspediten" (p. 456) or "dickere und flachere sog. Craspediten" (p. 455) of Stolley.
?1979	*Dichotomites* sp. nov. aff. *perovalis* Luppov, Bogdanova and Lobachova, Pl. III, figs. 2a, 2b.

Holotype. Original specimen of Koenen's (1902) Pl. 47, figs. 3, 4 preserved in collections of the GIG, Cat. No. 457-25.

Locus typicus. Stadthagen (brick factory Moeller).

Stratum typicum. Unknown.

Material. 8 specimens from Hasslage (Nord), Stadthagen, Sachsenhagen (Canal), Wiedenbruegge and Ottensen. The material is from the middle-upper *Dichotomites*-Beds.

Diagnosis. Apparently medium-sized species with slender and high whorls, which are strongly involute. The venter is narrowly arched. The umbilicus is very narrow and funnel-like. The sculpture is relatively fine and dense. Adult external suture line essentially like the typical variant of the *P. ivanovi* suture.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
BGR, kv 127	93	19(20)	30(32)	44(47)	29	38
BGR, kv 129	111	24(22)	37(33)	50(45)	—	—
BGR, kv 130	86	17(20)	28(33)	41(48)	25	33

Description. The three specimens BGR, kv 127, Pl. 23, fig. 2; BGR, kv 130, Pl. 23, fig. 1; and BGR, kv 128, unfigured, in which the last whorl is occupied by the living chamber do not appear to be adults. The other specimens are septate to the end. Therefore, the size of an adult shell is not known, but is estimated to be about 170 mm. The holotype is an extreme variant with an obtusely arched venter. The other material has, in contrast, a narrowly arched ventral region. The flanks are directed more convergently and are more convex. The greatest width of the whorls is situated at the level of the umbilical shoulder.

The umbilical shoulder is broadly rounded and merges into an only moderately high umbilical wall, which is distinctly convex. As the involution of the shell is considerable (about 83 per cent), the narrow and only moderately deep umbilicus is funnel-like. It is also very uniformly shaped until late in ontogeny when it widens slightly because of an insignificant decrease in involution.

The adult external suture line of *P. perovalis* (Koenen) remains poorly known. Of its only two examples available in the personally studied material, the two oralmost sutures of BGR, kv 127, (Pl. 23, figure 2A; Figure 44a) are poorly preserved in the umbilical part while the terminal suture line of BGR, kv 128 (Figure 44b) lacks the most part of the ventral lobe and is otherwise poorly preserved, with the exception of its umbilical part. The two previously described and figured suture lines of the holotype (Koenen, 1902, p. 87, 88; Pl. XLVII, fig. 3) were not re-studied on the original. Judging by their photograph, these incomplete sutures are inaccurately, and in part erroneously (especially the second auxiliary lobe of the posterior suture that is shown to include the bulk of the fourth lateral saddle), outlined by the draftsman. In spite of these defects, these sutures do not seem to differ materially from those of BGR, kv 127 and BGR, kv 128. All presently known examples appear to be early adult rather than terminal adult sutures because of the character of the sculpture on the living chambers of the specimens concerned.

These examples of *P. perovalis* sutures are of the same general type as the adult external sutures of *P. hollwedensis*, *P. polytomus* (except for the suture of BGR, kv 126), *P. glaber* n. sp. and *P. ivanovi*. They only differ

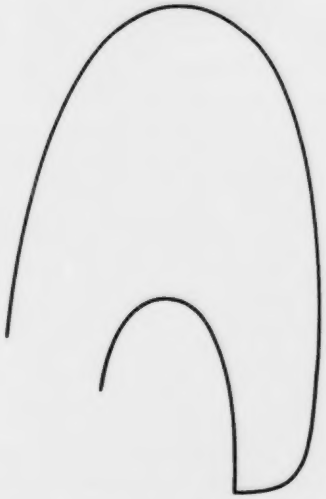


Figure 43. Cross-section of *Prodichotomites perovalis* (Koenen). BGR, kv 330 from Diepenau clay pit, Northwest Germany. Lower upper Valanginian, xl.

from them in a few details that are described below. The more complexly denticulated, more slender-lobed variant of *P. flexicosta* suture (Figure 40a) is also similar. *P. perovalis* suture is quite unlike the adult external sutures of *P. complanatus*, *P. fissuratus* and the sturdy lobed, relatively simply denticulated variant of *P. flexicosta* suture (Figure 40b).

The sutures of *P. perovalis* resemble particularly closely the adult external suture of *P. glaber* n. sp. (Figure 41b). The latter is indistinguishable from them in the shape, proportions and degree of denticulation of its lobes and saddles, with the exception of the third auxiliary lobe and the sixth lateral saddle. This lobe of *P. glaber* n. sp. is a small, simple structure that is separated from the umbilical seam by a rather wide (?nearly completely exposed) sixth lateral saddle. The only known example of the well preserved, third auxiliary of *P. perovalis* (i.e. of BGR, kv 128; Figure 44b) is considerably larger, distinctly denticulated and situated at the very umbilical seam with no part of the sixth lateral saddle visible. The same appears to be true of the strongly weathered third auxiliary of BGR, kv 127 (Figure 44a).

Where *P. hollwedensis* and *P. polytomus* are concerned, the suture of *P. perovalis* resembles most closely that variant of their suture which is characterized by parallel-flanked, less complexly and less deeply denticulated lobes (e.g. Koenen, 1902; Pl. XLVI, fig. 4; this paper Figure 38a). From these sutures the suture of *P. perovalis* appears to only differ in:

1. An apparently stronger ascendant (at 20 to 30 degrees in relation to the corresponding shell radius), essentially straight lateral part of the suture including the first auxiliary lobe;
2. The somewhat more retractive (or descendant) orientation of the remaining umbilical part of the suture that is also straight and meets its lateral part at an obtuse angle; and
3. A distinctly lesser width of all lateral saddles in comparison with their equivalents in *P. hollwedensis* and *P. polytomus*.

The degree of constancy of these distinctions cannot be apprised at the present.

The more complexly denticulated and slender lobed variant of adult external suture of *P. flexicosta* apparently differs from that of *P. perovalis* first of all in its persistently ascendant orientation and approximate straightness (compare Figure 40a with Figures 44a, 44b). This contrasts with the above described marked and rather abrupt change of the direction in the middle part of the *P. perovalis* suture. Furthermore, the lobes of this variant of the *P. flexicosta* suture are, as a rule, somewhat more sturdy than their equivalents in the *P. perovalis* suture. In the instances when the lobes are comparably slender those of *P. flexicosta* distinctly contract adorally and are considerably more deeply and complexly denticulated (Figure 40a).

The distinctions of the sutures of *P. perovalis* and *P. ivanovi* shall be discussed below in the description of the latter species.

The sculpture is relatively fine and dense. Bullae appear already early in the ontogeny. It is impossible to ascertain the exact shell size when this happens but they appear to be present already at a shell diameter of about 30 mm. They are delicate but typically developed at all later growth stages. In the specimen BGR, kv 130 (Pl. 23, fig. 1) the last preserved whorl carries 21 bullae while the penultimate whorl carries 23 bullae. It is an extreme variant with numerous bullae, as their number averages less per whorl. Specimen BGR, kv 127 (Pl. 23, fig. 2) has 17 bullae on the last preserved whorl. In BGR, kv 127 and BGR, kv 130 the bullae are invariably elevated and sharpened on the last preserved whorl. They are comma-like while the primary ribs of earlier whorls are oriented radially. The bullae only extend for a short distance onto the umbilical wall where these extensions peter out within its outer third.

The ribs of the early whorls are arranged in tridichotomous bundles. At a shell diameter of 60 to 80 mm the ribbing habit becomes more irregular while the number of ribs per bundle increases. Only a few of the secondary ribs are still connected with the bullae in this growth stage. Some secondary ribs are weakened and only intercalated. There are usually 7 to 8 tertiary ribs per bundle; the additional ones are predominantly intercalated. Their subdivision or starting points are not situated at the same level. The sculpture of this growth stage corresponds to that of ammonites figured by Koenen (1902) as *"Polyptychites" polytomus* (Pl. 46, figs. 3, 4) and *"P." ramulosus* (Pl. 46, figs. 1, 2). It is designated herein as the heteroptychous sculpture (Figure 6). This type of sculpture appears already in the progressive variants of *P. hollwedensis* and is the most advanced sculptural style in the genus *Prodichotomites*. A moderate weakening of sculpture on the flanks may occur in some specimens. The ribs are more or less pronouncedly bent forward on the venter.

Affinities and diffferences. P. perovalis is the intermediate member of the evolutionary lineage *P. polytomus*-*P. ivanovi* which occurs in the middle part of the *Dichotomites*-Beds (upper Valanginian). Accordingly it is connected by transitions with these two forms. *P. polytomus* is more broadly umbilicate, has lower and thicker whorls and a coarser sculpture than does *P. perovalis*. *P. ivanovi* is still more narrowly umbilicate and has still more slender and relatively higher whorls than *P. perovalis*. Furthermore, it is a considerably larger shell. Finally, it exhibits a stronger weakening of the sculpture on the flanks and, on the whole, a finer and denser sculpture. *P. glaber* is larger, thicker and more widely umbilicate. Furthermore, it is distinguished by a stronger weakening of the sculpture on the flanks. The principal distinctions of *P. perovalis* from *P. complanatus* and *P. fissuratus* consist in its more regularly shaped and funnel-like umbilicus and an entirely different adult external suture line.

P. perovalis was so far only found in the Lower Saxony Basin.

Prodichotomites ivanovi (Aristov 1974)

Pl. 24, figs. 2-4; Pl. 25, fig. 1; Figures 44c, 45, 46a-46c.

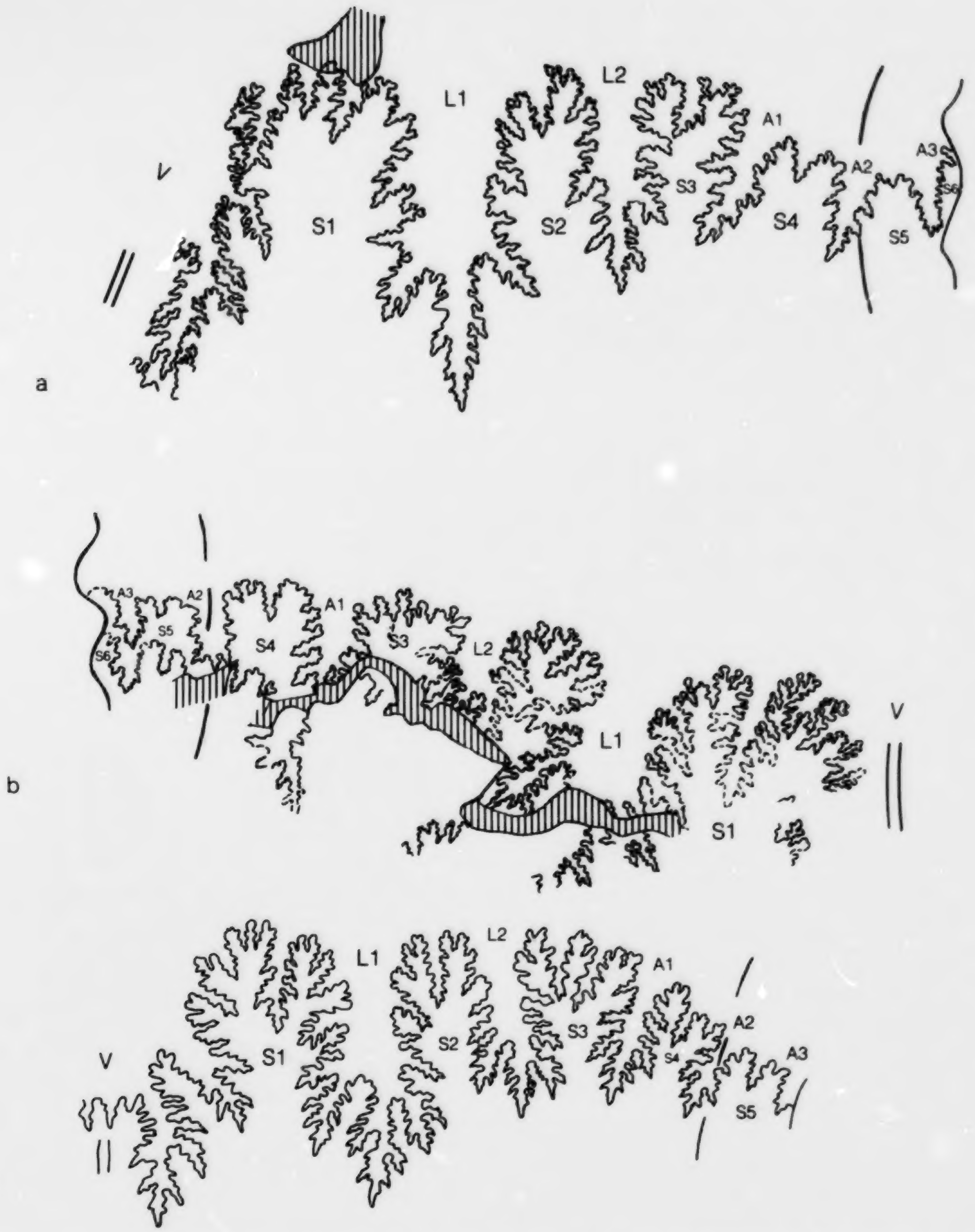


Figure 44. **a**. *Prodichotomites perovalis* (Koenen). BGR, kv 127. Early adult (oralmost but not terminal adult) external suture line at the whorl diameter of 32 mm, x 2.5. **b**. *Prodichotomites perovalis* (Koenen). BGR, kv 128. Two early adult (oralmost but not terminal adult) partial external suture lines at the whorl diameter of 37 mm, x2 (appr.). **c**. *Prodichotomites ivanovi* (Aristov). BGR, kv 331. Adult external suture line at the whorl diameter of 106 mm, x1.

1937 "Craspediten der oberen Dichotomiten-Schichten" Stolley, p. 455.

1974 *Homolsomites ivanovi* Aristov, p. 152, 153; Pl. XIV, figs. 1, 2; Pl. XV, figs. 1-3.

Holotype. The specimen figured by Aristov (1974, Pl. 14, No. 1/151).

Locus typicus. The former Village Krest, near Yaroslavl (USSR).

Stratum typicum. *Homolsomites bojarkensis* Zone. "Lower Hauterivian" sensu Aristov (1974) but actually upper Valanginian (Jeletzky, 1973, p. 73; Kemper and Jeletzky, 1979, p. 16, Figure 9).

Material. 13 specimens from the localities Ottensen, Diepenau? and Hasslage (North) in Germany from the upper upper Valanginian *Dichotomites bidichotomoides* Zone.

Diagnosis. A large species with very slender and very high whorls. The umbilicus is very narrow and shallowly funnel-like. Whorls are very strongly and regularly involute. The sculpture is dense and delicate; it tends to be weakened on the flanks. The adult external suture line varies from one essentially similar to that of *P. perovalis* to one including four to (rarely) five auxiliary lobes. The latter advanced variant is also characterized by lobes that are uniquely complex, deeply incised, and slender for the genus, equally uniquely narrow saddles, and the presence of the first and second auxiliaries on the flank.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
BGR, kv 309	107	18(17)	37(35)	52(49)	28?	37?
BGR, kv 310*	160	26(16)	55(34)	79(49)	39	50
BGR, kv 313*	175	29(17)	58(33)	88(50)	—	—
BGR, kv 308	110	22(20)	37(34)	51(46)	26?	—

*The measurements are not reliable.

Description. The state of preservation of the German specimens is indifferent, which makes it impossible to measure the adult size of the species. It is estimated at approximately 200 mm. The living chamber, like that of other species, occupies approximately the whole of one whorl.

The whorls are high and slender. The flanks are moderately convex and strongly convergent adventrally. Therefore, the venter is very narrowly arched. The convexity and the convergence of the flanks increase in the adult (e.g. BGR, kv 310; Pl. 25, fig. 1B or BGR, kv 331; Figure 45). The flanks may be almost level and subparallelly oriented in the early growth stages (e.g. BGR, kv 311; Pl. 24, fig. 4B). Addorsally the flanks merge across a rounded umbilical shoulder (Pl. 25, fig. 1A) into a low, moderately steeply oriented and feebly convex umbilical wall. The involution is considerable (about 87 percent) and the umbilicus is very narrow (about 17 percent). The umbilicus is funnel- rather than steplike because of the rounded character of the umbilical shoulder.

Seven well preserved, complete to nearly complete, adult external suture lines of the Northwest German representatives (e.g. BGR, kv 308, 309, 310, 311, 313, 331 and 350) of *P. ivanovi* and the adult external suture of its Central Russian holotype were studied. These sutures are generally similar to the previously described, most complexly and deeply denticulated and, at the same time, most slender lobed variant of adult external suture lines known in *P. hollwedensis* (Figures 38b, 38c) and *P. polytomus* (Koenen, 1902, p. 91, Pl. XLVI, fig. 1).

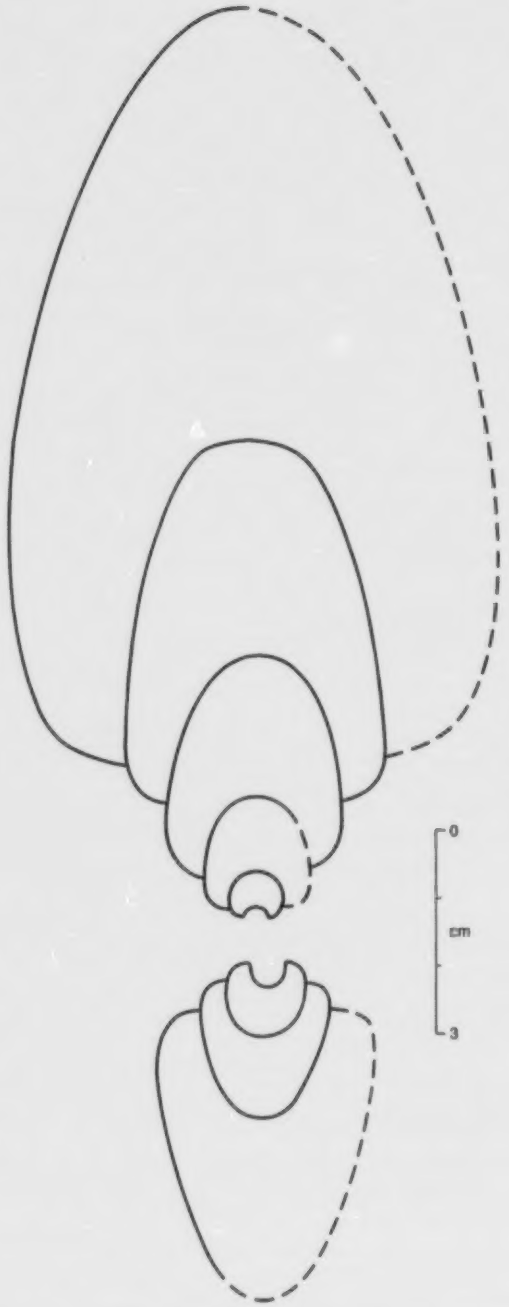


Figure 45. Cross-section of *Prodichotomites ivanovi* (Aristov). BGR, kv 331, x1. From Ottensen clay pit, Northwest Germany. Upper upper Valanginian. The linear scale provides the degree of the reduction.

This general type of adult external suture line also characterizes all other presently known Northwest German *Prodichotomites* species, except for *P. complanatus* and *P. fissuratus* (compare Figure 41a and Koenen, 1902, Pl. V, figs. 2, 12, 13). Though rather constant in the above mentioned general aspects, the adult external suture of *P. ivanovi* is extremely variable in most of its other morphological details.

One extreme, so called **typical variant** is represented by the sutures of the holotype (Aristov, 1974, Pl. XIV, fig. 2; Pl. XV, fig. 3), BGR, kv 311 (Figure 46c), BGR, kv 313 (unfigured), and BGR, kv 331 (Figure 44c). It is actually a morphologically and presumably evolutionarily conservative variant because of the presence of only three auxiliary lobes and other features discussed below that ally it with that of the immediately ancestral *P. perovalis*, that of still older representatives of the principal lineage of *Prodichotomites*, and ultimately with that of *Polyptychites* ex gr. *multicostatus* (Figure 11). This variant is typified by the almost undistinguishable sutures of the specimens BGR, kv 313 and BGR, kv 331 which shall be discussed summarily. These sutures apparently occur on the oral half of adult penultimate whorls.

The imaginary line connecting the tops of the first three lateral saddles of these sutures ascends at an angle of 15 to 20 degrees and is approximately straight. Then it bends rapidly backward and becomes subradial over the first auxiliary lobe. This subradial orientation then persists to the umbilical seam.

The first auxiliary lobe is always situated on the adumbilical part of the flank and is separated from the umbilical shoulder by the whole width of the fourth lateral saddle (Figures 44c, 46c). The second auxiliary is always situated on the crest of the umbilical shoulder while the third is either cut in two by the umbilical seam (e.g. Figure 44c; Aristov, 1974, Pl. XIV, fig. 2) or is situated just at that seam (Figure 46c) with only a sliver of the sixth lateral saddle visible behind it.

The shape, proportions and degree of denticulation of lobes and saddles of the typical variant are rather variable. The specimens BGR, kv 313 and BGR, kv 331 (Figure 44c) have particularly slender and long lobes with the length/width ratio that is greater than that known in any other *Prodichotomites* species and approaches that of the progressive variant described below. For example, the length/width ratio of all lobes of BGR, kv 331 is around 6. However, the length/width ratio of all lobes decreases to about 4 in the holotype of *P. ivanovi* and to about 3 in BGR, kv 311 (Figure 46c). However, the sturdiest known lobes of the specimen BGR, kv 311 may not be representative either of the typical variant or of the entire species because of its much younger individual age than the almost equally sturdy lobed holotype.

The flanks of all lobes are mostly subparallel. However, their slendermost examples may contract slightly to distinctly adorally (e.g. in BGR, kv 331; Figure 44c) while their sturdiest known examples may taper slightly to distinctly adapically (e.g. in the holotype; Aristov, 1974, Pl. XV, fig. 3).

All saddles of the variant are characteristically more narrow than their equivalents in other *Prodichotomites* species. The first and second lateral saddles are, as a rule, more narrow than the preceding lobes. The third to fifth lateral saddles are appreciably wider than the preceding lobes but, generally speaking, less so than the equivalent saddles of other *Prodichotomites* species. The width of saddles increases adapically in the typical variant. The saddles and lobes, both, are strongly subdivided by long and slender, first order lobules which are, in turn, incised. Only the third auxiliary lobe is exceptional in being simply and shallowly incised. The terminations of all lobes are trifid. All larger and smaller lobules of the saddles are markedly incised. Except for the fifth lateral saddle, the narrow appearance of all saddles is increased by a deep penetration by larger lobules.

The outlined and overpainted external suture of the Yaroslavl holotype (Aristov, 1974, Pl. XV, fig. 3) agrees well with the Northwest German examples of its typical variant, except for the first lateral saddle. This saddle is presumed to be strongly altered either by a photographic arrangement or by a deformation. However, Aristov's (1974) Fig. 2 of Pl. XIV also exhibits a peculiar subdivision of this saddle. It is uncertain whether or not this saddle really is built as it appears to be. The central lobule of the second lateral saddle also appears to differ from its equivalents in the Northwest German examples of the typical variant (Aristov, 1974, Pl. XV, fig. 3). However, this is obviously simulated by an erroneous outlining and overpainting of this lobule as evidenced by its dimly visible true outline.

Generally speaking, the typical variant of the *P. ivanovi* suture is indistinguishable from the adult external suture of *P. perovalis* in most of its morphological features (e.g. the orientation, number of auxiliary lobes, relative width and ornamentation of lobes and saddles etc.). The slendermost-lobed examples of this sutural variant of *P. ivanovi* typified by BGR, kv 331 (Figure 44c) can only be distinguished from the still imperfectly known suture of *P. perovalis* in:

1. A considerably more complex and deeper denticulation of all its elements; and
2. A considerably greater slenderness of all its lobes combined with a considerably to appreciably lesser width of the first and second lateral saddles.

However, the most conservative examples, typified by the holotype of *P. ivanovi* (Aristov, l. cit.) and the BGR, kv 311 (Figure 46c) do not seem to differ from the adult external suture of *P. perovalis* in either of these respects.

From the extreme, still insufficiently understood variant of *P. polytomus* and *P. hollwedensis* suture discussed in p. 95-96 and reproduced in Figures 38b, 38c the typical variant of *P. ivanovi* suture differs significantly in:

1. A considerably lesser relative width of the third and fourth lateral saddles and their considerably more adventral positioning. The fourth lateral saddle of *P. ivanovi* is always situated entirely on the adumbilicalmost part of the flank while that of *P. polytomus* and *P. hollwedensis* is situated already on the umbilical wall; and
2. A considerably more adventral positioning of the first and second auxiliary lobes. The second auxi-

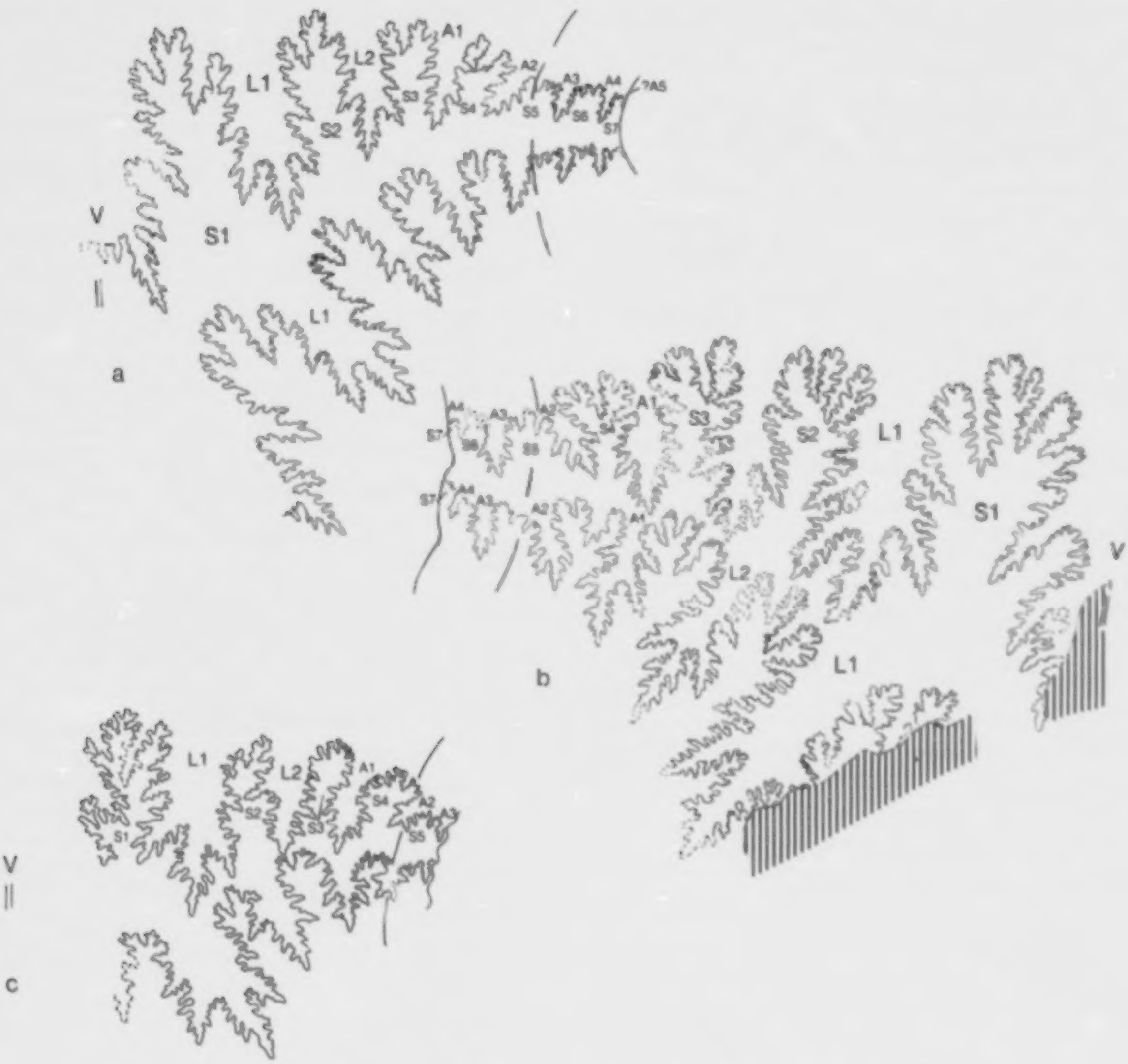


Figure 46. Adult external suture lines of *Prodichotomites ivanovi* (Aristov 1974). **a.** kv 309, Ottensen (compare, Pl. 24, fig. 3). Earlier adult sutures of the entirely septate (?adult penultimate) whorl at wh of about 50 mm, x 1.2; **b.** kv 308, (compare Pl. 24, fig. 2), Ottensen. Advanced (?terminal) adult sutures of the entirely septate whorl fragment that probably precedes immediately the adult living chamber at the wh 80 mm, x 1; **c.** kv 311, Ottensen, (compare Pl. 24, fig.,4), early adult sutures of an early intermediate whorl at wh 23 mm; x 2. These sutures have much more sturdy lobes and only three auxiliaries and so are much less advanced morphologically than the sutures of kv 309 and kv 308. They are only comparable to the most conservative advanced adult sutures of kv 331 (Figure 44c) in the number of auxiliary lobes but not in the degree of slenderness of their lobes. All specimens are from upper upper Valanginian.

liary of *P. ivanovi* always is bisected by the umbilical shoulder while that of *P. polytomus* and *P. hollwedensis* is situated entirely on the umbilical wall.

The other extreme, the so called **progressive variant** of *P. ivanovi* suture is so far only known in its Northwest German examples (e.g. BGR, kv 308, 309, 310, and 350). It differs from the adult external sutures of all other *Prodichotomites* species and from the so called typical variant of *P. ivanovi* suture in the presence of the fourth and rarely (in the BGR, kv 309 only; Figure 46a) the fifth auxiliary lobes on the inner part of the umbilical wall. Furthermore, it differs in the positioning of the first and second auxiliaries on the adumbilical part of the flank. Only the third auxiliary is situated on the outer half of the umbilical wall (e.g. Figures 46a, 46b). Finally all lateral saddles of the progressive variant are distinctly more narrow than the equivalent saddles of the typical variant and those of all other *Prodichotomites* species.

The above discussed, extremely great morphological variability of adult external suture line of *P. ivanovi* is regarded tentatively as an intraspecific feature. It does not appear to be correlative with morphological changes of any other features of our species and its extreme morphological examples intergrade freely in the Northwest German specimens at least. Furthermore, there is no indication that the typical and progressive variants of *P. ivanovi* suture are restricted to different stratigraphic levels in the Lower Saxony basin. However, the stratigraphic control there is rather limited and future collecting may necessitate a revision of this conclusion.

The sculpture is relatively fine and dense. The principal sculptural elements are developed as delicate but very sharp principal ribs (Pl. 24, fig. 4A) until a shell diameter of about 35 mm. At this growth stage there are 24 of these ribs, which are already comma-like. They become higher, and therefore transform into bullae, on the succeeding whorls. Specimen kv 309 (Pl. 24, fig. 3A) has 18 bullae on the last whorl, which can be tentatively interpreted as the adult penultimate whorl. According to the evidence provided by other specimens, this number represents an average for the penadult and adult growth stages. The strength of curvature of the bullae varies. Their extensions on the umbilical wall disappear within the outer third of the wall. The bullae become very weak in the adult.

The bullae of early whorls subdivide into 2-3 slender secondary ribs, each of which bifurcates into 2 tertiary ribs approximately at mid flank. Until a shell diameter of about 40 mm the subdivision points of these tertiaries are situated at the same height (e.g. kv 311; Pl. 24, fig. 4A). The ribbing habit becomes more irregular and more complicated on the following whorls, in particular because of the appearance of additional ribs (Pl. 24, figs. 2, 3A). This results in the appearance of sculpture of a *polytomus-ramulicosta* type, which was described and defined earlier. Thereafter, on the penultimate whorl, begins a more or less pronounced weakening of the sculpture on the flanks, which results in a *Neocraspedites*-like appearance of the adult growth stages (Pl. 24, fig. 2; Pl. 25, fig. 1). The remaining ribs on the ventral shoulder and venter are, as a rule, pronouncedly bent forward (Pl. 25, fig. 1).

Affinities and differences. The shape and proportions of the shell of Yaroslavl specimens agree well with those of German specimens, so far as it is possible to judge in view of the deformed state of the former. The weakening of the sculpture on the flanks starts at varying diameters in the German specimens, but usually later than in the Yaroslavl ones where it commences at shell diameters of 60 to 80 mm. According to Aristov (1974), the rib bundles of the latter consists of polyptychously and bidichotomously arranged ribs. This evidently refers to the small fragment reproduced in Aristov's Pl. XV, figs. 2a, 2b. The size of this specimen corresponds approximately to that of the specimen reproduced in Pl. 24, figs. 4A, 4B of this paper, which also exhibits some quasibidichotomous bundles. However, the branching is more regular than that in the Yaroslavl specimen. Aristov's (1. cit.) schematical drawing of rib-branching pattern (Pl. XV, fig. 2a) is confusing and the similarities of the rib-branching pattern in the Russian and German specimens is greater than the drawing indicates. However, there are differences, especially in the closer adumbilical position of the branching points in the figured fragment from Yaroslavl. If one takes into account the range of variation of the mode of splitting of the ribs in the German material of the species, the differences of the two specimens compared above must be rated as insignificant. As already pointed out, the same applies to the morphological distinctions of the adult suture of the holotype from the sutures of the NW German representatives.

The species is the terminal member of the *hollwedensis-polytomus-perovalis- ivanovi* evolutionary lineage and is connected by transitional forms with the preceding species *P. perovalis*. *P. ivanovi* differs from the other species of the lineage in having the largest shell, narrowest umbilicus, the most slender and highest whorls, and the uniquely slender-lobed and complexly denticulated adult external suture that commonly has four auxiliary lobes. The similarly large *P. glaber* is considerably thicker. Further, the degree of narrowing of its umbilicus and the height of its whorl remain well below those of *P. ivanovi*. The *Neocraspedites*-like ammonites of the early late Valanginian (i.e. *P. complanatus*, *P. undulatus*) differ in their smaller shell size and the evolutionary grade characterized by a late ontogenetic decrease of involution of their whorls.

The late late Valanginian species *P. ivanovi* occurs in the Lower Saxony Basin (NW Germany) and in the Yaroslavl' district of the Russian Platform.

Prodichotomites grotriani
(Neumayr and Uhlig 1881)

*1881 *Olcostephanus Grotriani* Neumayr and Uhlig, p. 153, Pl. 24, fig. 1, 1a (non Pl. 23, fig. 1).
*1881 *Olcostephanus obsoletecostatus* Neumayr and Uhlig, p. 153, Pl. 25, fig. 1.

Lectotype. The original of Neumayr and Uhlig's (1881), Pl. 24, fig. 1.

Locus typicus. Ludwig-Mine, Salzgitter district.

Stratum typicum. "Hilseisenstein". The Hils iron ore is a condensed horizon, so the age of the species is unknown.

Discussion. The lectotype is lost and its figure in Neumayr and Uhlig (1881) is undoubtedly "beautified" and therefore falsified. Hence, it is impossible to define the species with confidence. This is all the more true because even the age of the type specimen cannot be established. *P. grotriani* is, therefore, a very questionable and problematic species. The extraordinary size of the lectotype is remarkable. It is the second largest *Prodichotomites* ever found in NW Germany after the previously mentioned specimen in the Wiedenroth collection. It has a shell diameter of 270 mm.

The sculpture is of the *polytomus* type. The combination of features present in *P. grotriani* does not occur in any other species. *P. grotriani* is, therefore, definitely a valid species. It was evidently confined to special environment in the southern part of the Lower Saxony Basin. The species *P. obsoletecostatus* is placed herein in its synonymy.

Canadian Taxa

Genus *Polyptychites* Pavlow 1892

Polyptychites keyserlingi (Neumayr and Uhlig 1881)

Pl. 32, figs. 1, 2, Figure 47a.

Synonymy for North America
(see pages 56-57 for a complete Eurasian synonymy)

?1964	*Polyptychites* cf. *keyserlingi* Jeletzky, p. 40, Pl. VI, fig. 2A, 2B.
1973	*Polyptychites (Polyptychites) keyserlingi* Jeletzky, p. 67, 68, Pl. 1, fig. 2; Pl. 3, fig. 2a, 2b.
1975	*Polyptychites keyserlingi* Kemper, p. 248.
1977	*Polyptychites (Polyptychites) keyserlingi* Kemper, p. 3, 4.

Material. Two fairly well preserved specimens from the Deer Bay Formation, GSC loc. 82695, Amund Ringnes Island, Sverdrup Basin. One of them GSC Cat. 32592 was originally figured by Jeletzky (1973, Pl. 2, fig. 2; Pl. 3, fig. 2a, 2b) and is refigured herein (Pl. 32, fig. 1). The other is figured here (Pl. 32, fig. 2)

One strongly deformed, only tentatively identified specimen from GSC loc. 27884 in the basal Beattie Peaks Formation, Peace River Foothills, northeastern British Columbia figured by Jeletzky (1964, p. 17, 40; Pl. VI, fig. 2).

Diagnosis. See the description of the Northwest German material.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
GSC Cat. 32592	74	22(30)	24(32)	30(41)	30(41)	37(50)
GSC Cat. 77095	(74)	23(31)	—	28(38)	—	36(49)

Description. The German material demonstrates the great variability of *P. keyserlingi*, and this is also seen in the differences in sculpture and width of shell exhibited by the two definitively identifiable Canadian specimens, which are approximately of the same size (Pl. 32, figs. 1, 2). Specimen GSC Cat. No. 32592 is the better preserved of the two. Both specimens retain about a half whorl long remnant of the presumably adult living chamber.

In specimen GSC Cat. No. 32592 the whorl section varies from approximately semicircular to faintly narrow arched and is distinctly wider than high. The umbilical wall is distinctly inclined rather than steep and the umbilical shoulder is broadly rounded. The umbilicus is step-like.

An early appearance of bullae is an important sculptural feature. Well defined bullae are present on at least the three outermost whorls (including the adult last whorl). There are 18 bullae on the penultimate whorl and 13 to 14 on the last whorl, where the bullae are distinctly sharper and more strongly developed.

The character of supplementary ribs is only visible on the last whorl where their number fluctuates between 4 and 5 per bullae. The posterior rib bifurcates. the remaining 1 to 2 tertiary ribs are attached to the anterior secondary. This bundling habit agrees with that of the adult growth stage of *P. keyserlingi*.

Specimen GSC Cat. No. 77095 is somewhat wider with a more narrowly rounded venter. The other features of the shell's shape are not recognizable because of its deformation (Pl. 32, fig. 2). The bullae number 8 per half whorl on the last whorl so that their number per whorl (16) is somewhat greater than in the other specimen. The bundling habit also differs. In the bundles situated about one-half of the whorl before the shell's end only the posterior secondary rib bifurcates higher on the flank. The other three secondary ribs originate directly in the bullae. The next two rib bundles consist of three bifurcating secondaries each. The last preserved rib bundle has a quasipolyptychous character, that is its supplementary ribs originate from the posterior rib and from the bulla itself.

No constrictions were observed on either specimen.

The external suture lines are clearly visible on the early part of the last whorl of each specimen (Pl. 32, figs. 1A, 1D; Figure 47a). The two lateral lobes and the first auxiliary lobe are situated on the flanks, with the first auxiliary lobe sitting on the top part of the bullae. The markedly widened saddle separating the first and second auxiliary lobes is bisected by the umbilical shoulder so that the remaining second and third auxiliary lobes are situated entirely on the umbilical wall. The third auxiliary lobe is situated just at the umbilical seam and is partly concealed by it. The two lateral lobes and the first auxiliary lobe are long, narrow, parallel-flanked structures that are only shallowly denticulated. The second and third auxiliaries are tack-like and only slightly notched. The saddles are approximately square and either slightly or considerably (the saddle separating the first and second auxiliary lobes only; Pl. 32, fig. 1A; Figure 47a) wider than the preceding lobes. The line uniting the tops of the two lateral and first auxiliary lobes is approximately straight and ascendant at 10 to 15 degrees in relation to the corresponding shell radius while that uniting the remaining auxiliary part of the suture line is slightly ascendant. The two parts meet at a very obtuse angle.

These suture lines are similar to those of morphologically and presumably phylogenetically advanced German representatives of *P. keyserlingi* (e.g. *P. k.* var. *suessi* Koenen 1902) (see p. 62 for further details).

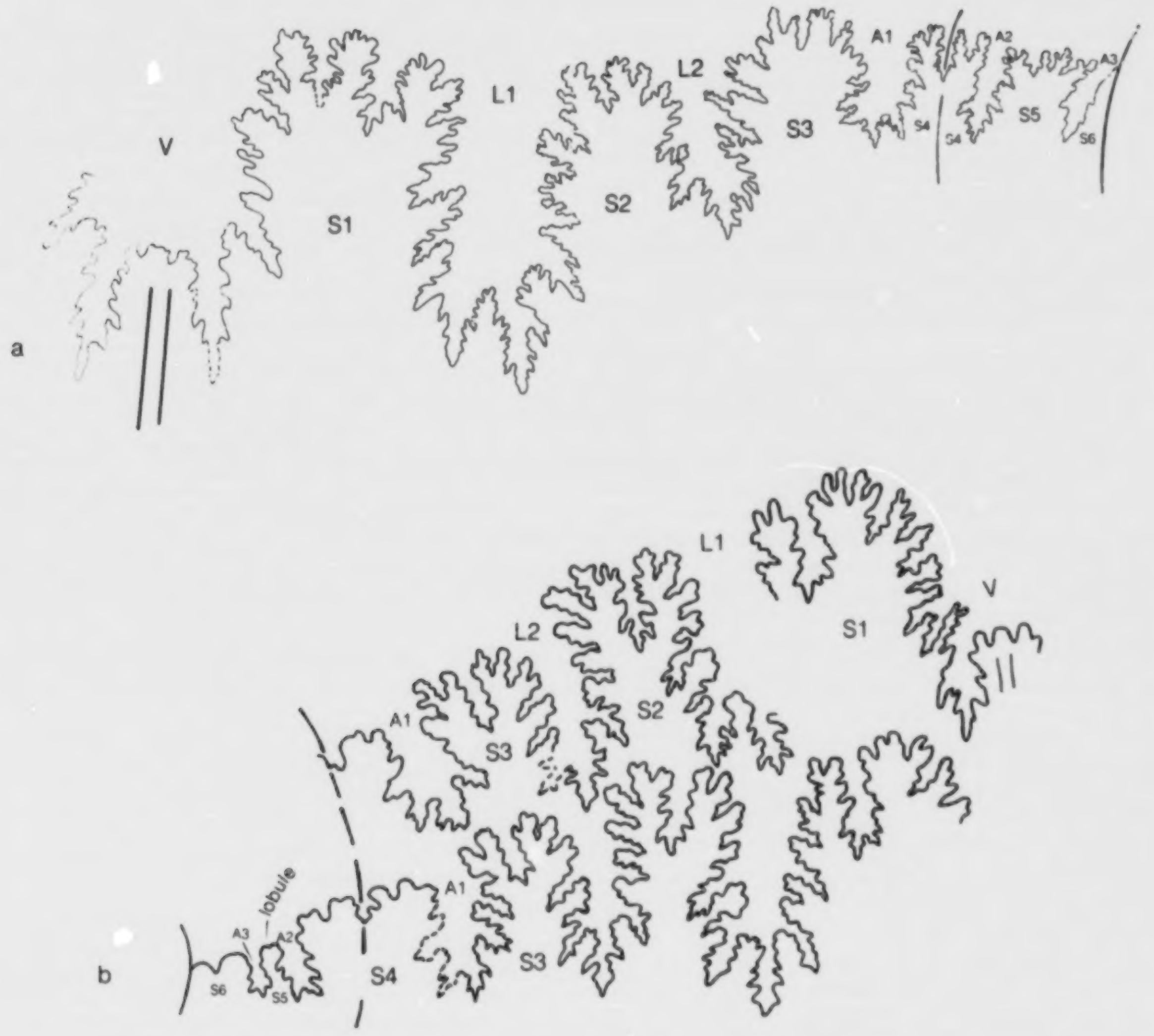


Figure 47. Adult external suture lines of the Canadian *Polyptychites* species. **a**. *P. keyserlingi* (Neumayr and Uhlig 1881). Specimen GSC Cat. 32592 (Pl. 32, fig. 1). Fifth suture from the end of the adult phragmocone at the shell diameter of 60 mm (est.), x 2 (approx.). **b**. *P. tschekanovskii* (Pavlow, 1914). Specimen GSC Cat. 77109 (Pl. 41, fig. 1). Advanced adult suture exposed on the oral part of adult penultimate whorl at the whorl diameter of about 80 mm (Pl. 41, fig. 1), x 1 (approx.).

Affinities and differences. The Canadian *P. keyserlingi* differs from Northwest German specimens mainly in their whorl section. The latter are less narrowly arched while exhibiting a greater tendency toward subparallel flanks. However, they are characterized also by wh smaller than wth. The total number of supplementary (i.e. secondary and tertiary) ribs is generally less in the German material, usually not exceeding 4 per bundle. Further differences are mentioned in the description of German material (see p. 62).

Stratigraphy and age. The two specimens from the Deer Bay Formation at GSC loc. 82695 were collected by the pilot of R. Thorsteinsson's field party in 1968. No data are available about the exact location and stratigraphic level of this fossil locality. However, its rich ammonite fauna includes, in addition to *P. keyserlingi*, *Polyptychites canadensis* Kemper & Jeletzky 1979, *P.* aff. *hapkei*, *P.* aff. *tschekanovskii* (Pavlow 1914) and *Siberiptychities (Siberiptychites)* n. sp. aff. *stubendorffi* (Schmidt 1872). These represent at least two late early Valanginian polyptychitinid associations, that were indiscriminately collected on the float. The locality is inferred to be high in the formation and to include beds equivalent to Beds 8, 9 and 14 of Kemper's (1977, p. 3, Figure 3) Section 74/11. *P. keyserlingi* and *S. (S.)* n. sp. aff. *stubendorffi* presumably represent an association either equivalent to or only slightly younger than Kemper's Bed 14 fauna. The remaining ammonites represent the next younger beds, 8-9 which were named the Tschekanovskii Beds by Kemper & Jeletzky (1979, p. 13, Figure 9). The Tschekanovskii Beds are situated at the lower/upper Valanginian boundary, and are dated tentatively as latest early Valanginian (Kemper & Jeletzky loc. cit.; this paper, Figure 62). The association of *P. canadensis* and *P.* aff. *tschekanovskii* with *P.* aff. *hapkei* at GSC loc. 82695 supports this dating. The same is, furthermore, true of the absence of representatives of *Prodichotomites* and *Ringnesiceras* at this locality. It is suggested accordingly that the GSC loc. 82695 does not include any ammonites derived from equivalents of the basal upper Valanginian Bed 7 of Kemper (1977, p. 3, Figure 3), that was designated the *Ringnesiceras (Ringnesiceras) pseudopolyptychum* Beds by Kemper & Jeletzky (1979, p. 13, Figure 9).

Whatever the exact stratigraphic position of the specimens of *P. keyserlingi* may be, they prove the presence of the interregional Eurasian *Polyptychites keyserlingi* Zone in the Sverdrup Basin. This zone is presumably present also in the basal part of the Beattie Peaks Formation in the Peace River Basin of northeastern British Columbia (Jeletzky, 1964, p. 17, 40, Pl. VI, fig. 2).

Because of the morphologically and, presumably, phylogenetically advanced nature of the Canadian specimens, they are inferred to represent the highest Northwest German beds where *P. keyserlingi* is abundant (i.e. the *Polyptychites clarkei* Subzone; see Figure 62). Their horizon may correlate with that part of the North Siberian *Polyptychites michalskii* Zone where *P.* ex gr. *keyserlingi* are stated to occur frequently (Gol'bert et al., 1981 and this paper, Figure 62).

Polyptychites aff. *hapkei* n. sp.

Pl. 43, figs. 2A-2C.

Synonymy for North America
(see page 81 for a complete Eurasian synonymy)

1973	*Polyptychites* ex aff. *tschekanovskii* Jeletzky, p. 68.
1975	*Polyptychites sphaeroidalis* (= *P. tschekanovskii* Pavlow 1914) Kemper, p. 248.
1977	*Polyptychites sphaeroidalis sphaeroidalis* Kemper, p. 4.

Material. One fragment, comprising about one-half of a whorl from GSC loc. 82695.

Diagnosis. See description of Northwest German material.

Measurements. At Wh of 50 mm Wth comprises 74 mm (height/width ratio about 68 percent).

Description. The only fragment available does not exhibit any traces of a suture line. It is therefore interpreted as representing some part of a presumably adult living chamber. As indicated by the measurements, this broadly rounded whorl is considerably wider than high. Numerous, delicate supplementary ribs branch off the bullae. The bullae are well defined but not very strongly developed, as is characteristic of the species. The ribbing is so indistinctly developed that it is impossible to observe exactly the number of supplementary ribs and their bundling habit.

The indistinct and variable (?adult) character of the sculpture precludes definitive identification. Nevertheless, there is little doubt that the specimen is either specifically identical with or closely related to *P. hapkei* n. sp. from Northwest Germany. Its close affinity or specific identify with *P. hapkei* is indicated by the following characters:

1. A similarly large size and globular shape of the whorl;
2. A similarly narrow umbilicus.
3. A similarly high-arched (Roman arch-like) cross-section of the whorl combined with fairly rounded umbilical shoulders;
4. A comparable number of similarly shaped umbilical nodes, which number 12 to 14 per whorl in both forms;
5. Both forms become semismooth to quite smooth on penultimate and/or ultimate whorls.

P. hapkei is an index fossil of the highest zone of the lower Valanginian in Northwest Germany (Kemper 1976; 1977, Figure 2). However, it persists also into the basal beds of the upper Valanginian. The presence of a solitary fragment in some, still undetermined part of the upper Deer Bay Formation indicates the occurrence of the *P. hapkei* Zone in the Sverdrup Basin (Figure 62).

The affinities with and distinctions from *P. tschekanowskii* are discussed in the description of the latter species. The shape and proportions of the adult growth stages of *Polyptychites* ex *gr. orbitatus* may be similar to those of the Canadian fragment. However, these forms bear a considerably more refined and differently bundled sculpture on the early and intermediate growth stage (see p. 75).

Tschekanovskii Group

Polyptychites tschekanovskii Pavlow 1914

Pl. 40, fig. 1,; Pl. 41, fig. 1; Pl. 42, fig. 2; Pl. 67, fig.1; Figure 47b.

1872	*Ammonites polyptychus* var. *Stubendorffi* (in part) Schmidt, p. 133, Pl. 11, fig. 13.
1914	*Polyptychites Tschekanovskii* Pavlow, p. 34-36, Pl. VIII, IX, X.
non 1973	*Polyptychites* ex aff. *tschekanovskii* Jeletzky, p. 68.
1975	*Polyptychites sphaeroidalis* (= *tschekanovskii* Pavlow) Kemper, p. 248.
1977	*Polyptychites (Polyptychites) sphaeroidalis tschekanovskii* Kemper, p. 4.

Holotype. The original of Pavlow's (1914) Pls. VIII-X is the holotype of *Polyptychites tschekanovskii* by monotypy.

Material. A large specimen from Amund Ringnes Island (Ke 74/11/8; GSC loc. 91302), which is well preserved to its last whorl.

Locus typicus. The watershed of Khatanga and Anabar Rivers in the proximity of the Salt Range (Pavlow, 1914, p.34).

Diagnosis. A very large species of the genus *Polyptychites* with wide but narrowly-arched rather than low outer whorls. The sculpture is relatively coarse. A generally *Polyptychites hapkei*-like adult external suture line is relatively more deeply and richly denticulated and its lateral part is, as a rule, more markedly ascendant. It has a considerably wider and more richly denticulated fourth lateral saddle and a relatively much more narrow, only slightly notched fifth lateral saddle.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
GSC 77109 (GSC Loc. 91302)	220	67(30)	64(29)	90(41)	96	(123)

Description. An outstanding distinction of the species is its huge size, which is reached also by other Arctic species of *Polyptychites*. The fully septate holotype (Pavlow, 1914, p. 35, Pl. IX) has a maximum measurable shell diameter of 225 mm. That of the Canadian specimen, which includes a part of the living chamber, is estimated at 260 mm.

The specimen from Amund Ringnes Island is septate at least to the beginning of its outermost half whorl. Its whorls are relatively high and narrowly rounded for the proportions which are characteristic for the species. However, it agrees completely with holotype in this respect. The whorls are considerably wider than high. The greatest width of the whorl is situated at the level of the umbilical shoulder.

The character of the early whorls is unfortunately unknown in the Canadian specimen. However, it is elucidated, in part, by Pavlow's (1914, p. 35, Pl. X) description and illustrations of the earlier whorl of the holotype, which is as follows (Jeletzky's translation from Russian): "The youngest whorl, a part of which became exposed during the preparation of the specimen, has a whorl diameter of about 80 mm with the corresponding width of 51 mm. This whorl has a deep and steep umbilicus ornamented by fifteen umbonal ribs, which are strongly inclined backward and thicken toward the umbonal shoulder. At that shoulder they split into bundles of very strongly expressed, ridge-like ribs, which are slightly inclined forward and equally thick throughout their length. Every bundle begins with two ribs, of which either only the posterior or only the anterior, or finally both, bifurcate again at about one-third up the whorl's height. The ribs cross the siphonal side without any weakening. In addition to the bundles that begin in the umbonal ribs, there are intercalated dichotomous bundles. In other words, this sculpture exhibits 4 types of bundles — virgatothomous, polyptychitoid, bidichotomous and the supplementary dichotomous bundles. I was only able to observe this sculpture on the younger half of this whorl as its other half remained concealed by the next whorl".

"The next whorl is 145 mm in diameter and has a relatively deeper and more nearly perpendicular umbilicus. The first half of this umbilicus is ornamented by eleven umbilical ribs, which are inclined backward. On the second half of the umbilicus the umbonal ribs become obliterated in its depth while acquiring the character of transversally elongated and backwardly inclined umbonal nodes. The bundles of outer ribs either issue from these nodes or begin in the intervals between them. These bundles are not as well defined as on the preceding whorl as the umbonal ends of the outer ribs are weakened and the character of their connection with the umbonal nodes becomes obscure. It is, however, possible to see clearly that some of the ribs bifurcate at a level one-third up the flank. As one can see from the dimensions and the drawing, the whorl becomes higher and narrows up in the siphonal area of this growth stage. However, one has to point out that the true shape of its cross-section is somewhat distorted by the pressure. The original shape of the cross-section on the siphonal side had an arch of a greater radius."

This larger intermediate whorl of the holotype (Pavlow, 1914, Pl. X, figs. 2a, 1b) apparently overlaps with the earliest exposed part of the Canadian specimen (Pl. 40, fig. 1) the sculpture of which is described below.

The deep umbilicus of the Canadian specimen suggests that its concealed inner whorls are also relatively wider than the outer whorls. The umbilical shoulder is broadly rounded on the early whorls but becomes more narrowly rounded on the last whorl. The umbilical wall is steep (and even slightly concave?) in the juvenile growth stage but becomes somewhat more oblique and slightly convex in the adulthood. The umbilicus of the Canadian specimen is, as a whole, step-like rather than funnel-like in spite of its great depth.

The sculpture of the earliest visible whorl of the Canadian specimen consists of bullae and supplementary ribs which branch off the former. The whorl that precedes the last preserved half whorl has 12 bullae, which bend forward on the umbilical wall. These comma-like extensions of the bullae are even more strongly expressed on the exposed part of the preceding whorl. The bullae are relatively high and narrowly sharp-topped on the early part of the last completely preserved whorl but become wide and low on its anterior half. No constrictions were seen on the Canadian specimen and the holotype of the species appears to lack them also.

The sculpture of the Canadian specimen is only observable on the last one and a half whorls. At first rib bundles with four supplementary ribs (one anterior and one posterior bifurcating element which subdivide at different levels) alternate with bundles of a *hapkei* type (i.e. tridichotomous), which consist of three almost identical bifurcating elements that subdivide at the same level. One of these elements is often only intercalated, instead of being connected, with the bulla. Thereafter the sculpture rapidly becomes irregular. Farther adorally it soon disappears (at about the beginning of the last preserved whorl) in a zone situated between the bullae and the middle of the flank. This weakening of the sculpture on the flank increases with age so that the last preserved segment (i.e. the living chamber; Pl. 40, fig. 1; Pl. 41, fig. 1) is almost smooth, except for the widely spaced bullae. However, it is assumed that the non-preserved ventral shoulder and venter of this segment of the living chamber still retained the supplementary ribs. Another remarkable feature is that the ribs of the last completely preserved whorl (i.e. penultimate) are strongly arched forward on the flank but cross the venter transversally to subtransversally.

The only known example of the adult external suture line of *Polyptychites tschekanovskii* (Figure 47b) belongs to the previously defined advanced type of *Polyptychites* suture line with two lateral and three auxiliary lobes. Only second and third auxiliaries are situated on the umbilical wall. The ventral lobe is considerably wider and somewhat longer than the first lateral lobe. The two are about equally complexly and deeply denticulated. The first lateral saddle is somewhat wider than the ventral lobe but considerably wider than the narrow-stemmed and parallel-sided first lateral lobe. This saddle is denticulated by a large and fairly deeply frilled first order lobule situated much closer to its adumbilical side and three or four small second order lobules. Its top is either adorally convex or ascendant adventrally.

The first lateral lobe is about two and a half times longer than wide and symmetrically trifid. The second lateral saddle is either about as wide as the first lateral lobe or up to one and a half times wider than it. Its flat, subradially oriented top is subdivided in two subequal parts by a large lobule similar to the principal lobule of the first lateral saddle and a couple of small, second order lobules.

The second lateral lobe is an almost exact replica of the first, except for being slightly smaller (Figure 47b).

The third lateral saddle matches closely the second lateral saddle in its relative width, shape and the denticulation of its slightly adorally convex top.

The first auxiliary lobe again matches closely the first and second lateral lobes in its overall shape, proportions and the degree of denticulation. It is only slightly shorter and, possibly, somewhat wider than the second lateral lobe. Unlike the first and second laterals that are oriented almost exactly in the direction of the shell's growth, the first auxiliary is markedly to pronouncedly adventrally inclined. This auxiliary is situated at the top (i.e. at the branching point) of the umbilical node (Pl. 41, fig. 1; Figure 47b).

The fourth lateral saddle is strongly widened relatively to the preceding lateral saddles. It occupies the rest of the umbilical node and all of the narrowly rounded umbilical shoulder. This saddle is about two and a half times wider than the preceding third lateral saddle and is subdivided in four parts by three lobules. Its median asymmetrically trifid lobule is two to three times larger than the flanking simple, adapically rounded lobules.

The second auxiliary lobe is situated on the outermost part of the umbilical wall. It is about three times smaller than the first auxiliary and markedly oblique adventrally. It appears to be bifid rather than trifid but the few examples seen are all poorly preserved.

The third auxiliary lobe is separated from the second auxiliary by an exceptionally narrow, barely notched fifth lateral saddle. This lobe may either be situated just before the umbilical seam (it may even be partly covered by it) or within the inner half of the umbilical wall. If the latter (Figure 47b), it is separated from the umbilical seam by the greater part of the sixth lateral saddle that is subdivided in two by a small and simple, roundtipped lobule. The fourth auxiliary was not seen in any of the exposed suture lines of the specimen.

The tops of both lateral lobes and the top of the first auxiliary lobe form a somewhat adorally convex line which protrudes forward at 10 to 15 degrees. Beginning with third lateral saddle (i.e. that separating the second lateral lobe from the first auxiliary lobe), the imaginary line connecting the tops of the auxiliary elements swings rapidly into a subradial orientatiion. This orientation is reached at about the outer flank of the second auxiliary lobe and then maintained to the umbilical seam.

So far as it is known (Pavlow, 1914, p. 36), the partial external suture line of the North Siberian holotype seems to be similar to the above described suture line of the Canadian specimen.

The agreement of the Canadian specimen with the outermost whorl of the holotype of *P. tschekanovskii* is extremely close.

The species is so far only known from the Sverdrup Basin and Northern Siberia but it is likely to occur in other high Boreal basins. During his 1982 visit to Leningrad Kemper saw in the collections of the State Institute for Study of the Arctic Seas of U.S.S.R. a great number of large ammonites which obviously belong to *P. tschekanovskii*, but they have yet to be studied in detail.

Affinities and differences. *Polyptychites tschekanovskii* is obviously closely related to *P. hapkei* and is interpreted as its offspring (Figure 11). The two possess a similar bundling habit and the adult external suture of *P. tschekanovskii* is nearly identical with that of the most advanced representatives of the progressive variant of *P. hapkei* suture (see p. 85, 86). The *P. tschekanovskii* suture differs from that of the conservative variant of *P. hapkei*, that of the advanced and conservative variants of *P. keyserlingi*, and from that of *P*. ex gr. *multicostatus* in the same way as does the suture of the most advanced representatives of *P. hapkei*. Its points of similarity with the sutures of *P. keyserlingi* and *P*. ex gr. *multicostatus* appear to be a matter of homoeomorphy only.

In spite of its close similarity with *P. hapkei*, *P. tschekanovskii* possesses an *Euryptychites*-like juvenile growth stage absent in the former species, is 2 to 3 times larger, and has a much wider and more complexly denticulated fourth lateral saddle (compare Figures 36c and 47b). These distinctions are ample for a full specific separation of the two. *P. tschekanovskii* cannot be confused with any other Northwest European *Polyptychites* species. Its morphological differences from *P.* aff. *tschekanovskii* and *Polyptchites* n. sp. A are discussed in the descriptions of the latter forms.

Age and correlation. The Canadian specimen of *Polyptychites tschekanovskii* was found in the Bed 8 of the Section Ke/74/11 (Kemper, 1977, p. 3, Figure 3) that forms part of the *Polyptychites tschekanovskii* Beds. These beds are inferred to be correlative with the lower part of the Hollwedensis Zone and to be of the latest early Valanginian age (Figure 62).

Polyptychites aff. *tschekanovskii* Pavlow 1914

Pl. 33, fig. 1; Pl. 34, figs. 1A, 1B; Pl. 35, figs. 1A-1C; Figure 48a

1977 *Polyptychites (Polyptychites)* n. sp. aff. *lamplughi* Kemper, p. 4

Material. One specimen from GSC loc. 82695. GSC Cat. 77097.

Locus typicus. Amund Ringnes Island, N.W.T., near the northern tip of the island; Lat. 78°40'N.; Long. 98°00'W.

Stratum typicum. Somewhere in the upper part of the Deer Bay Formation. Most likely from an equivalent of the fossil beds 8-9 of Kemper (1977, Figure 3) and of the latest early Valanginian age.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
GSC Cat. No. 77097*	210	47(22)	71(39)	93(44)	80	103

*The measurements may be unreliable because of a lateral deformation of the specimen, the degree of which was impossible to ascertain.

Description. The only available entirely septate phragmocone has the maximum shell diameter of slightly under 220 mm. Therefore, the shell diameter of the complete specimen must have reached at least 270 mm. The shell is wide and *Euryptychites*-like in the early growth stages (for example, wh: wth is 15:24). The whorls become more narrow-arched and relatively higher beginning with the shell diameters of about 50-60 mm. At the shell diameter of about 130 mm, the outermost part of the whorl has the ratio-wh:wth of 62:66 mm. This ratio is then approximately maintained to the oral end (further examples are 74:81 mm and in the table of measurements above). The largest width of the whorl is situated at the level of the umbilical shoulder. The somewhat asymmetrical shape of the intermediate and outer whorls and their internally mashed up appearance suggest that these width/height ratios are distorted by lateral compression of the specimen, which was probably lower and wider-whorled originally. The whorls are very involute for the genus (but only moderately involute in general terms; see p. 16) and the umbilicus is correspondingly small with about 22 per cent. The umbilical shoulder is broadly rounded. In the intermediate and late whorls it merges gradually into the umbilical wall, which is not steeply oriented but inclined at about 70 degrees. In spite of the rounded umblical shoulders, the umbilicus has a step-like rather than funnel-like appearance. No constrictions were observed.

The external suture line (Figure 48a) is proportioned, denticulated and oriented almost exactly like the previously described external suture of the Canadian representative of *P. tschekanovskii* (compare Figure 47b). The two even share the extremely narrow, barely notched appearance of the fifth lateral saddle and appear to differ only in a much greater relative width of the fourth lateral saddle of *P. tschekanovskii* and a much more complex denticulation of its sixth lateral saddle. The apparently more simple denticulation of the ventral and first lateral lobes and the intervening first lateral saddle of *P.* aff. *tschekanovskii* (Figure 48a) appears to be caused by their less satisfactory preservation only.

There are 12 to 13 bullae on the last whorl. However, the preceding half whorl carries 8 bullae. The bullae are flat swellings, which are oriented transversally to the direction of the growth of the shell and are not bent comma-like forward on the umbilical wall. They are relatively weakly developed and become transformed into much more strongly expressed, better rounded elevations on the last preserved half whorl only.

The distinct development of the tertiary ribs is remarkable. These ribs arise by either bifurcation or intercalation at about the middle of the flank. The points of subdivision are situated at about the same level. The secondary ribs are unequal as some of them are more prominently built than the others. As in *P. hapkei*, the early half of the last preserved whorl bears two to three bifurcating secondaries for each bulla. Some of these bifurcating ribs are intercalated instead of being connected with the bullae. The subdivision of ribs becomes indistinct on the oral half of the last preserved whorl because of the disappearance of the more feebly developed secondary ribs and the exclusive preservation of the more strongly developed ribs. The subdivision of ribs obviously becomes more irregular on this half of the whorl. Furthermore, the sculpture is characterized by slight forward bends of the ribs on the venter.

Affinities and differences. The predominantly regular ribbing habit, the bundles of which consist largely of 3 bifurcating secondaries per whorl with the subdivision points situated at the same level on the flank, resembles very closely that of the youngest known *Polyptychites* species of Northwest Germany, such as *P. orbitatus* (Koenen) and *P. hapkei*. The tendency toward the development of a very refined sculpture is also present in these youngest known *Polyptychites* forms of Northwest Germany. Therefore one can infer the derivation of *P.* aff. *tschekanovskii* from the *P. hapkei* species group. However, like *P. tschekanovskii*, *P.* aff. *tschekanovskii* differs in the presence of a very early appearing *Euryptychites*-like growth stage. This sets the Canadian forms of *P. tschekanovskii* species group apart from its European relatives.

The specimen differs from *P. canadensis* Jeletzky and Kemper 1979 in its wide-whorled, *Euryptychites*-like juvenile growth stages and in its relatively wider whorls in general. However, it is the funnel- rather than step-like umbilicus that is the most distinctive feature. *P. balkwilli* n. sp. differs in the same features and is considerably more slender than *P. canadensis*.

The originally assumed affinity to *P. lamplughi* (Pavlow) (see Kemper, 1977) was not confirmed by the closer study of our specimen. The difference in the width of the umbilicus (33 per cent of the shell diameter in *P. lamplughi*, 22 per cent in *P.* aff. *tschekanovskii*) is significant. Further differences are present in the whorl section and in the sculpture, as the sculpture of *P. lamplughi* is of a *keyserlingi* type. Finally, the adult external suture of *P. lamplughi* is like that of the progressive variant of *P. keyserlingi*.

The distinctions from *P.* n. sp. A are discussed later.

The morphological distinctions of the adult external suture line of *P.* aff. *tschekanovskii* from that of *P. tschekanovskii* may be interpreted as suggestive of its being a closely related new species. However, the range of variation of *P.* aff. *tschekanovskii* and *P. tschekanovskii* sutures is not known. All other apparent morphological distinctions of *P.* aff. *tschekanovskii* from *P. tschekanovskii*, such as its relatively more narrow and higher intermediate and adult whorls and its more shallow umbilicus, may possibly be caused by its postmortal deformation. *P.* aff. *tschekanovskii* is described accordingly in the open nomenclature pending the discovery of additional, better preserved material.

Age and correlation. See the discussion of the stratigraphy and age of the GSC loc. 82695 in the description of Canadian representatives of *Polyptychites keyserlingi*.

Polyptychites n. sp. A

Pl. 52, figs. 1A-1F; Figure 48b, 48c.

Material. Fragments of a solitary specimen GSC Cat. 77121 from NW part of Amund Ringnes Island, GSC loc. 91301 (Ke-74/11/7); Lat. 78°38'20"N; Long. 97°56'W.

Locus typicus. Bed 7 of the upper Deer Bay Formation (Kemper, 1977, Figure 3), of an early late Valanginian age.

Description. The specimen consists of about 7/8 of an intermediate whorl with some attached fragments of two preceding whorls and those of the next following whorl. The incomplete state of preservation precludes a complete evaluation and a definitive taxonomic assignment of this completely septate specimen. It belongs undoubtedly to one of the very large Arctic species of *Polyptychites*.

The innermost visible whorl is approximately twice as wide as it is high but cannot be measured accurately. The very low-arched venter is *Euryptychites*-like and is inseparable from the flanks. The umbilical wall and shoulders are almost regularly rounded and very indistinctly delimited from the flanks. The sculpture is too poorly preserved to be described in full, but the secondaries of this whorl and those of the preceding whorl (preserved as an imprint inside it) have distinct but broad forward bends on the venter.

The succeeding whorl has the same *Euryptychites*-like cross-section as the earliest preserved whorl. The width is about 31 mm while the height is only 18 mm at the earliest preserved part of the whorl. The early parts of the next succeeding whorl have the same proportions. However, the more adoral cross-sections gradually become relatively higher and higher and acquire better delimited flanks and umbilical wall. This results in a *Polyptychites*-like cross-section of the later part of this almost complete whorl (Pl. 52, fig. 1B, 1D).

The following measurements of the height/width ratio were obtained at a shell diameter of 130 mm: wh 1: wth 1 = 36: 50 mm and wh 2: wth 2 = 49:59 mm. The whorls are still considerably wider than high. Farther adorally the cross-section becomes gradually higher until it is nearly as high as wide at its oralmost undeformed part. This rapid increase of the whorl height is the most distinctive characteristic of the form. At this advanced growth stage, the distinctly convex flanks converge gradually but increasingly strongly adventrally from the level of maximum diameter which is situated at the umbilical shoulder. The regularly arched venter merges imperceptibly into the upper flank without forming any ventral shoulders. The umbilical wall of the preceding covered whorl is subperpendicular and approximately flat.

The moderately wide and step-like but moderately deep umbilicus exposes one-seventh to one-eighth of the preceding whorl which is ornamented by closely spaced, narrow and sharp-topped bullae. Wherever observable, these bullae persist across the umbilical wall to the umbilical seam.

The exposed, almost complete whorl, where the whorl shape and proportions change drastically, is ornamented by approximately 14-15 umbilical bullae which straddle the umbilical shoulder. On the adapical part of the whorl these bullae are comma-like (forwardly concave) and extend somewhat obliquely across the umbilical wall to the umbilical seam gradually attenuating in this direction. Farther adorally the length of the bullae decreases while their height increases gradually until they are transformed into high and sharptopped, elongated nodes on the oralmost preserved part of the whorl. These enlarged bullae end on the outer part of the umbilical wall leaving its inner half smooth. The rib bundles of the exposed whorl (Pl. 52, fig. 1C, 1E) consist of three secondaries arising directly out of their bullae on the adumbilicalmost part of the flank. Most of these secondaries bifurcate again high on the flank producing a somewhat irregular *hapkei*-like bundling habit. One or rarely two ribs may occur between the bundles. These intercalated ribs may or may not bifurcate. The ribs cross the venter of the exposed whorl in well defined but broad forward loops without any weakening in the middle (Pl. 52, fig. 1F). The same is true of the ventral rounding of the third preceding whorl (Pl. 52, fig. 1A) a short fragment of which is preserved as an impression inside the fragment of the second preceding whorl.

The secondary and tertiary ribs are only sharptopped and well defined on the earliest quarter of the previously discussed, exposed, almost complete whorl where their connections with bullae are also well defined. Farther adorally the ribs become more and more illdelimited and lowered on the flanks until they are barely distinguishable on the mid-flank of the last preserved quarter of the whorl. However, the ribs remain clearly defined to the oral end on the upper flank and the ventral part of the whorl, even if somewhat subdued in comparison with its earliest quarter. This produces a somewhat *Neocraspedities*-like effect. No constrictions were observed.

The completely exposed external suture line (Figures 48b, 48c) resembles very closely that of *P. tschekanovskii* and *P.* aff. *tschekanovskii* in its orientation, degree of denticulation and shape of the lobes, gradual decrease of the size of lateral elements toward the umbilical seam and apparently the number of lobes. It appears to have three auxiliary lobes but the structure interpreted as the third auxiliary is small and illdefined (roundtipped) in comparison with third auxiliaries of the other two forms. Furthermore, the saddle separating A2 and A3 is relatively much wider. The two lateral lobes and the first auxiliary lobe are situated on the flank of the whorl with the auxiliary being superposed on the topmost part and/or branching point of the bulla. The first and second auxiliaries are markedly adventrally inclined like those of *P. tschekanovskii* and *P.* aff. *tschekanovskii*. The two lateral lobes are much wider than those of these two species. The saddles are uniquely narrowed with the ventral saddle being appreciably more narrow than the first lateral lobe and much more narrow than the ventral lobe. The first and second lateral saddles are so narrow as to look slit-like. In consequence of that the lobules of the lobes flanking them mostly either touch or overlap (Figure 48b). The same appears to be true of the poorly exposed third and fourth lateral saddles. The fifth saddle (A2/A3) is markedly widened and is subdivided into three parts by tiny and simple lobules. It is because of the widening and subdivision of this saddle that the writers interpret the following simple lobe-like structure as the third auxiliary.

Affinities and differences. The wide shell of this indubitably larger species, the presence of an *Euryptychites*-like juvenile whorl shape combined with rapidly increasing height of its whorls, and the similiarities of its sculpture indicate its forming part of the *P. hapkei -P. tschekanovskii* species group. Like *P. tschekanovskii*, it differs from *P. hapkei* in being more than twice as large. Furthermore, it differs in the larger and more strongly elevated, node-like bullae of the last preserved whorl. The sculpture is generally considerably more delicate than that of *P. tschekanovskii*. Furthermore, it tends to disappear earlier (except for the bullae). The bullae are more elevated and are only feebly bent forward in a comma-like fashion. The umbilicus is more markedly step-like than that of *P. tschekanovskii*.

The whorls are broader and lower in comparison with those of *P.* aff. *tschekanovskii*. Furthermore the sculpture is more refined than that of the latter form while the bullae are more strongly developed and sharptopped.

P. n. sp. A differs from *P. canadensis* in its considerably broader (*Euryptychites*-like) inner whorls and in a rapid increase of the height of the whorl during the intermediate growth stages. Finally, it differs from all other *Polyptychites* species the authors are familiar with in an exceptional relative width of the lobes with correspondingly narrowed saddles. The latter are at least twice as narrow as the preceding lobes (e.g. the lateral saddle) and mostly are literally slit-like, with the lobules of flanking lobes commonly touching or overlapping.

There is little doubt that *Polyptychites* n. sp. A is a new species. However, the only known representative is too poorly preserved to serve as holotype of a new taxon, so it is described in open nomenclature pending the discovery of additional, better preserved material.

Remarks about the Polyptychites tschekanovskii-Polyptychites n. sp. A species group

P. tschekanovskii, *P.* aff. *tschekanovskii* and *P.* n. sp. A comprise a form group which is confined to the high-Boreal (or Arctic) basins and is characterized by the following morphological features shared by all its representatives:

1) The presence of an *Euryptychites*-like whorl section in the early to intermediate ontogenetic stages;
2) The presence of rib bundles of *P. hapkei* type at least in the intermediate growth stages; and
3) The gradual increase in whorl height in the late intermediate and adult growth stages that results in the adults looking like *P. keyserlingi*.

The first two of these features indicate derivation of this form group from *P. hapkei*. In *P. hapkei* the increase in whorl width towards *Euryptychites*-like proportions begins at shell diameters of 50 to 60 mm. In the Arctic form group, the earliest whorls recognizable in our material are already *Euryptychites*-like. This happens at shell diameters of 5 and 10 mm in *P.* aff. *tschekanovskii* and *P.* n. sp. A. The process of transformation is, therefore, transferred into the earlier ontogenetic stages in the Arctic form group. Unlike in *P. hapkei*, their late intermediate and adult growth stages become more narrow and relatively higher in comparison with their *Euryptychites*-like early growth stages.

Because of the scarcity of the material available it is not yet possible to make any definitive conclusion about the density of sculpture in our form group. At least *P.* aff. *tschekanovskii* and *P.* n. sp. A have a relatively refined sculpture on the early whorls.

The group differs from the other Arctic species group of *Polyptychites* characterized by huge size — namely that of *P. canadensis* — *P. balkwilli* — in a less step-like umbilicus and an *Euryptychites*-like shape of whorls of the early growth stages.

Canadensis-Balkwilli Group

Polyptychites canadensis Kemper and Jeletzky 1979

Pl. 30, fig. 4; Pl. 31, fig. 1A, 1B; Pl. 43, fig. 1, Pl. 46, fig. 2; Pl. 47, fig. 2; Pl. 48, fig. 2; Pl. 65, fig. 1; Figure 49a.

1977 *Polyptychites (Polyptychites) canadensis* Kemper, p. 5 (nomen nudum).

1979 *Polyptychites (Polyptychites) canadensis* Kemper & Jeletzky, p. 1, 2, Pl. 1, fig. 1A, 1B; Figure 2.

Origin of name. From the occurrence of the type material in Canada.

Holotype. The specimen GSC Cat. No. 61755 reproduced in Pl. 31, figs. 1A, 1B.

Material. Three specimens from three different fossil localities (GSC locs. 85025, 85059 and 93866) on Amund Ringnes Island, N.W.T.

Locus typicus. GSC Cat. 61755. Northwestern part of Amund Ringnes Island; Lat. 78°38’20”N; Long.91°56’W (holotype) and GSC Cat. 77113 (first paratype); Lat. 78°38’N; Long. 91°56’W.

Stratum typicum. Upper Deer Bay Formation, fossiliferous layers 7 to 9 of Kemper (1977, p. 5, Figure 3) and Kemper and Jeletzky (1979, p. 2, 13, Figure 1). Topmost lower and basal upper Valanginian (Figure 62).

Diagnosis. A very large *Polyptychites* species with a narrow umbilicus, which is pronouncedly steplike in the advanced growth stages. The whorls are narrow and high already in the early ontogenetic stages. The sculpture is dense but has relatively few bullae which are strongly comma-like (forward convex) on the umbilical wall. The adult external suture like that of *P. balkwilli* except for the smaller size, lesser denticulation, and less regular shape of the third auxiliary and the sixth lateral saddle combined with an occasional presence of the fourth auxiliary lobe.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
GSC Cat. 61755 (Holotype)	159	37(23)	55(35)	67(42)	49	69
GSC Cat. 77113 (Paratype)	ca 250	69	ca 82	105	—	119(?)

Description. The shell size of the paratype GSC Cat. 77113 exceeds 300 mm. As it is septate almost to the end, one has to infer a maximum diameter for the species of at least 400 mm, which means it is probably the largest *Polyptychites* species known.

The holotype comprises 5/6 of an intermediate whorl with considerable fragments of the preceding two whorls and small fragments of the third inner whorl. It's maximum diameter cannot be estimated. The preserved whorls are high and narrow. The innermost one is about as high as it is wide. The last preserved whorl is slightly higher than thick (wh:wth = 37:36) at a shell diameter of 85 mm. About one-half whorl farther this ratio is 55:49. About one-quarter whorl farther yet it is 62:60 and at the oral end of the last preserved whorl it is 69:72. On the earliest preserved whorl the flanks are more or less evenly convex throughout and merge imperceptibly into the similarly arched venter, which forms a regular Roman arch (Pl. 31, fig. 1B).

The early part of the succeeding whorl retains the above described proportions and cross-sections. Then the height gradually becomes somewhat greather than the width (at a diameter of about 150 mm) and the cross section becomes rounded-trapezoidal with distinctly flattened flanks and venter (see Pl. 31, fig. 1B). These whorl proportions and the cross-section are then retained throughout the outermost preserved whorl. However, the flattening of the flanks and venter increases gradually to the oral end of this whorl.

The broadly rounded umbilical shoulder merges into a relatively steeply oriented umbilical wall. In spite of a high degree of involution, a fairly wide periumbilical zone of the whorl remains exposed. The umbilicus is, therefore pronouncedly step-like. It is also shallow because of the width of the whorls which is small for the average values characteristic of *Polyptychites*.

The external suture does not differ materially from that of advanced NW German *Polyptychites* species (i.e. *P. hapkei* and *P. orbitatus* Koenen). As a rule, it has only three completely exposed auxiliary lobes in all known growth stages (Figure 49a). However, in the holotype the third umbilical lobe is followed by a completely exposed sixth lateral saddle followed by the outermost part of the fourth lobe bisected by the umbilical shoulder. See under the description of the suture line of *P. balkwilli* n. sp. for further details.

The ornament exhibits pronounced differences from one ontogenetic stage to another. At shell diameters of 40 to 50 mm it includes regular rib bundles consisting of two bifurcating secondary elements. The subdivision points of these elements are situated at about the middle of the flank. Such regular bidichotomous bundles alternate with more irregular bundles, in which the anterior bifurcating secondary is replaced either by a solitary secondary or by a bifurcating secondary, the subdivision of which is situated in the proximity of the bulla. The bullae of this growth stage are low and their length is oriented perpendicularly to the direction of growth. On the umbilical wall they are comma-like, bending in the direction of growth. 9 bullae were counted on a half whorl.

Further observations of the sculpture were only possible on the last preserved whorl. The bullae are considerably more strongly developed on this whorl and the width of intervals separating them has increased. The last preserved half whorl bears only 6 to 7 bullae. The ribbing of the last whorl is dense. An average of 2 secondary ribs branch from each bulla, while two to three tertiary ribs branch from these unequally strong secondary ribs. The subdivision points are situated predominantly

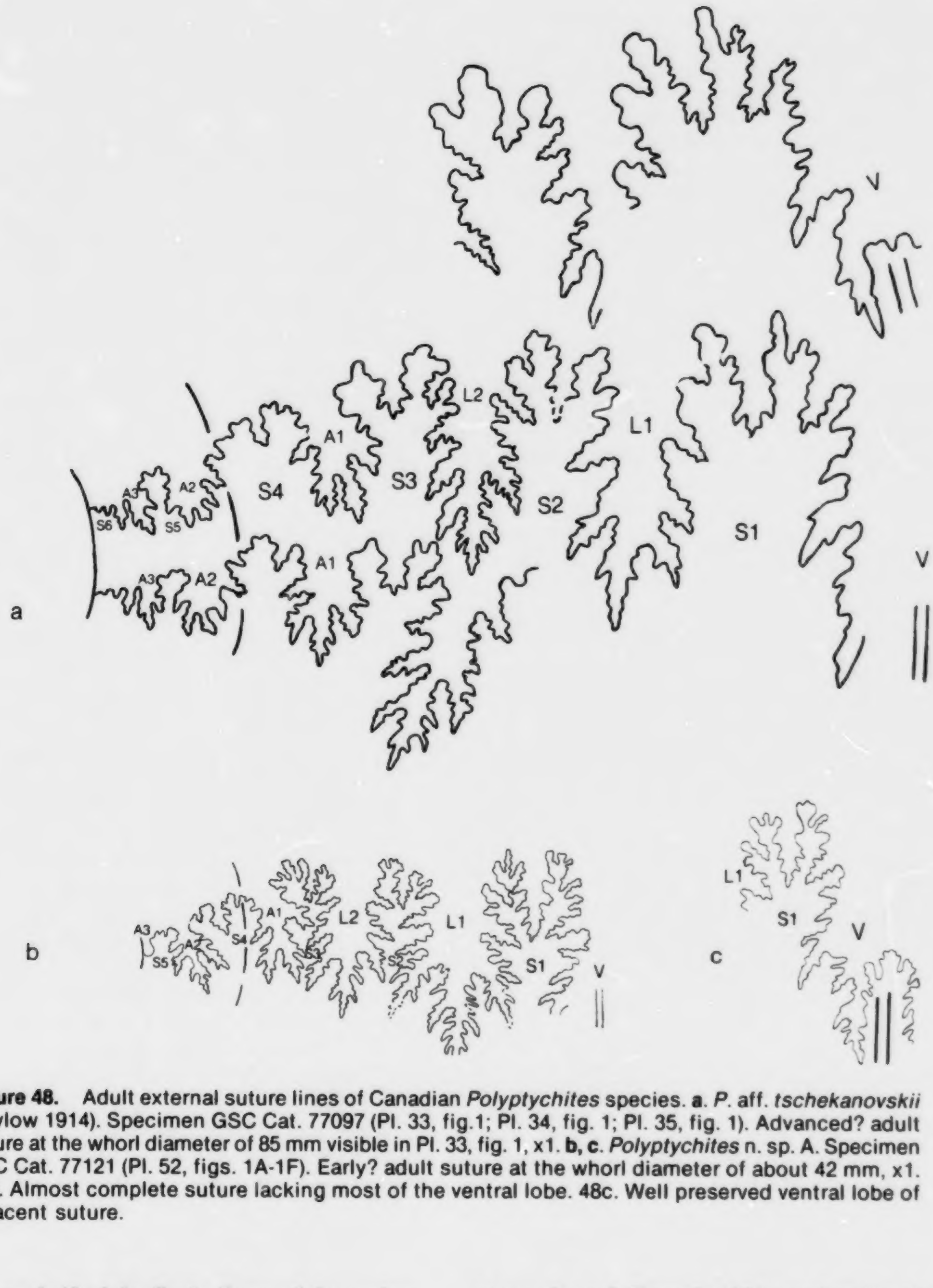


Figure 48. Adult external suture lines of Canadian *Polyptychites* species. **a**. *P.* aff. *tschekanovskii* (Pavlow 1914). Specimen GSC Cat. 77097 (Pl. 33, fig.1; Pl. 34, fig. 1; Pl. 35, fig. 1). Advanced? adult suture at the whorl diameter of 85 mm visible in Pl. 33, fig. 1, x1. **b, c**. *Polyptychites* n. sp. A. Specimen GSC Cat. 77121 (Pl. 52, figs. 1A-1F). Early? adult suture at the whorl diameter of about 42 mm, x1. 48b. Almost complete suture lacking most of the ventral lobe. 48c. Well preserved ventral lobe of adjacent suture.

within the outer half of the flank. Some of the tertiary ribs are only intercalated. The ribbing habit as a whole is irregular. The ribs exhibit a strong forward bend on the ventral rounding such as is otherwise particularly characteristic of the genera *Dichotomites* and *Prodichotomites*.

While the holotype represents the intermediate growth stages of the shell, the lst paratype (GSC 77113) exhibits the appearance of its adult growth stage. This specimen is a gigantic, somewhat fragmentary shell, which is septate to the end. Even should its oral end be situated just before the living chamber, the complete shell would certainly have a minimum diameter of 400 mm. The specimen exposes slightly more than one whorl presumed to be mostly the penultimate. About one-quarter whorl of one flank and about one-half whorl of the venter of the preceding whorl are visible where the outer whorl is damaged (Pl. 48, fig. 2).

The step-like shape of the shallow umbilicus is especially clearly developed in the lst paratype. The whorl flanks are more strongly convex than those of the holotype, but this convexity remains moderate for the conditions prevalent in *Polyptychites*. They converge gradually but increasingly strongly adventrally from the level of maximum diameter which is situated at the umbilical shoulder. The rather regularly arched venter merges imperceptibly into the upper flank without forming a ventral shoulder. The whorl width is only slightly greater than its height, even at a shell diameter of about 260 mm (wh:wth = 105:110 mm). The umbilical shoulder is almost regularly rounded instead of being abrupt.

The penultimate whorl of the lst paratype carries 10 low bullae. The first 5 bullae of this whorl still remain low, although somewhat more strongly expressed than before. They gradually increase in size and prominence adorally and become more widely spaced in this direction. This tendency probably continued on the missing living chamber. The sculpture disappears gradually on the last preserved whorl. It only remains preserved — as it is commonly the case in the genus — on the ventral rounding of this whorl. It is not possible to say anything about the bundling habit because of the weakening of the sculpture. Some more strongly expressed secondary and tertiary ribs are still visible at the beginning of the last whorl. Other weaker ribs of different length are intercalated between these stronger ribs.

The second unfigured paratype (GSC loc. 85059) consists of early whorls, which resemble strongly the corresponding whorls of *Prodichotomites* Kemper. The whorls are relatively narrow and high and have a narrowly rounded venter. The shape and sculpture of this paratype are similar to those of the holotype. The umbilical wall is low and gently inclined. The bullae are low and few in number, as is typical for this species group. The ribbing is fine and strongly arched forward on the ventral rounding (i.e. venter and ventral shoulders). It is weak and indistinct on the flanks at a shell diameter of 70 mm, which results in an indistinctness of the bundling habit. Some of the secondary ribs are broadly arched. The tertiary ribs are confined to the adventral halves of the whorls and are intercalated for the most part. Only a few of them can be connected with particular secondary ribs.

None of the studied specimens exhibit any constrictions.

Affinities and differences. See in the description of *Polyptychites balkwilli* n. sp.

Age and correlation. *Polyptychites canadensis* occurs in Beds 7-9 of the Section Ke-74/11 of Kemper (1977, p. 3, Figure 3) and so ranges through the *Polyptychites tschekanovskii* and *Ringnesiceras pseudopolyptychum* Beds (Kemper & Jeletzky, 1979, p. 13). Therefore, it is inferred to range through the equivalents of the entire Hollwedensis Zone and to occur in the latest early and earliest late Valanginian beds alike.

Polyptychites balkwilli n. sp.

Pl. 44, fig. 4; Pl. 45, fig. 1; Pl. 50, fig. 2A-2C; Figure 49b

1977 *Polyptychites (Polyptychites) balkwilli* Kemper, p. 4 (nomen nudum).

1979 *Polyptychites (Polyptychites) balkwilli* Kemper and Jeletzky, p. 1, 13 (nomen nudum).

Origin of name. For Dr. H. Balkwill, formerly with the ISPG, Geological Survey of Canada, presently with Petroleum Canada, Calgary, in recognition of his distinguished research on the geology of the Sverdrup Basin. Dr. Balkwill has efficiently supported the field work phase of this project.

Material. The following four specimens from Ellef Ringnes Island, N.W.T.: 1) A well preserved holotype GSC Cat. 77117 from GSC Loc. 91302 (= Ke 74/11/8); 2) A well preserved but incomplete lst paratype GSC Cat. 77120 from GSC loc. 85025; 3) A strongly laterally deformed 2nd paratype from GSC loc. 93753 (Ke 76/11/7-9); and 4) The third paratype from GSC loc. 93872 (Ke 76/11/7-9). The specimens 3 and 4 are poorly preserved.

Holotype. Specimen GSC Cat. 77117 reproduced in Pl. 44, fig. 4 and Pl. 45, fig. 1 is selected herewith as the holotype of *P. balkwilli* n. sp.

Stratum typicum. Upper Deer Bay Formation, fossiliferous layers 7-9 of Kemper (1977, Fig. 3) and Kemper and Jeletzky (1979, p. 13, Figure 1). Topmost lower and lowermost upper Valanginian (Figure 62).

Diagnosis. A very large *Polyptychites* species with high whorls, which are very slender for the genus. The umbilicus is step-like. The bullae are strongly comma-like (forwardly concave) on the umbilical wall. Adult external suture similar to that of *P. canadensis*, except for a larger size, stronger denticulation and more regular distribution of all elements situated on the umbilical wall.

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
GSC Cat. 77117	237	55(23)	80(34)	102(40)	—	(85)

Description. The holotype is septate to the end. The maximum preserved shell diameter of this specimen must be at least 270 mm. However, as attested by the remnants of the shell, the specimen extended for an additional whorl farther, so that the terminal diameter of the adult shell would be about 400 mm. The species is, therefore, one more of the largest known *Polyptychites*. The most striking feature of *P. balkwilli* is its high and slender whorls. The wh:wth ratio is 102:85 mm in the holotype. The flanks are but slightly convex and the venter is correspondingly narrowly rounded. The relatively narrow umbilicus has a strongly step-like appearance in spite of the broadly rounded umbilical shoulder and the pronounced involution of the whorl (about 83 per cent of the second penultimate whorl are covered by the last preserved whorl). The umbilical wall is rather steeply oriented. It is even slightly concave in the proximity of the umbilical seam on the last preserved part of the whorl of the holotype.

The advanced adult external suture of the holotype (Pl. 44, fig. 4 and Pl. 45, fig. 1; Figure 49b) has three auxiliary lobes. The lateral lobes and saddles are long. Because of a deep denticulation they appear to be narrow. All saddles are appreciably to much wider than the preceding lobes. The first lateral saddle is subdivided in three subequal parts by two approximately equally long and denticulated lobules. The second to fourth lateral saddles situated on the flank (i.e. L1/L2, L2/A1, and A1/A2) are all subdivided in two parts by solitary principal lobules. The fourth and fifth lateral saddles situated respectively next adventrally and next addorsally of the umbilical shoulder are asymmetrical (because of the adventral inclination of the second and third auxiliary lobes; see Figure 49b). However, they are clearly recognizable as saddles as they are not as strongly narrowed as their apparent equivalents in *P.* aff. *tschekanovskii* and are subdivided by well differentiated lobules (Figure 49b). The sixth and last auxiliary saddle is wide and almost completely exposed on the inner half of the umbilicus.

Both lateral and the outer two auxiliary lobes are expressly trifid. However, the trifid character of the third auxiliary is only indistinctly expressed because of its shortness and irregular shape. The two lateral lobes are orientated about parallel to the venter and the umbilical shoulder. However, the axes of the first and second auxiliary lobes are markedly adventrally inclined. This results in the imaginary adoral extensions of these two auxiliaries crossing the umbilical shoulder and in forming acute angles with it. The inclination of A1 is in order of 5 degrees while that of A2 reaches even 10 to 15 degrees. Such an oblique orientation of these two lobes is unusual. The considerably earlier adult sutures of the first paratype (Pl. 50, figs. 2B, 2C) does not differ materially from that of the holotype.

The sculpture is only feebly developed. The bullae are broad and low, except for the last half whorl where they become distinctly more strongly elevated. They are strongly comma-like (forwardly concave) on the umbilical wall. The last whorl carries 10 bullae. There are 7 very flat swellings on the early half of the penultimate preserved whorl which are also bent forward on the umbilical wall. The ribbing is only visible on the last preserved whorl of the holotype. However, it is already so weakened and indistinct there, that no reliable observations of the bundling habit and the numerical ratios can be made. It is only possible to assume that, on the average, 2-3 secondary ribs arise out of every bulla and that the tertiary ribs are intercalated between them on the more adventral part of the flank. The secondary and tertiary ribs comprising this "rib crown" are definitely distinctly arched forward on the ventral rounding of the intermediate growth stages. This adventral arching forward decreases on the last preserved whorl.

The first paratype (GSC Cat. 77120) displays well the early growth stages, which cannot be observed in the holotype. The specimen (Pl. 50, fig. 2A-2C) is septate to its end where its shell diameter measures 130 mm. Considerable segments of the last preserved whorl are either caved in or broken off. This whorl is also affected by deformations. It was, therefore, impossible to obtain any reliable measurements there. The last preserved whorl is evidently somewhat wider than high (wh:wth = 40:42?). The ventral rounding is invariably deformed. The only moderately convex flanks merge across a broadly rounded umbilical shoulder into a relatively low umbilical wall which is inclined at about 60 degrees. The moderately wide umbilicus is shallow and pronouncedly step-like. The whorls are evidently not pronouncedly involute. However, it was impossible to obtain exact measurements of the involution.

The penultimate preserved whorl carries 18 bullae, which rather represent strongly elevated primary ribs at its beginning but then become rapidly transformed into typically shaped bullae. 7 to 8 high and strongly expressed bullae occur on the first half of the last preserved whorl. They are pronouncedly comma-like (forwardly concave) on the umbilical wall. The strength of the bullae decreases considerably on the oral half of the last whorl. The distances between them increase at the same time.

The sculpture is strongly developed to a shell diameter of about 110 mm and then begins to weaken in a zone confined between the bullae and the middle of the flank. The bundling habit is irregular on the last preserved whorl. Its rib bundles include 2 to 3 secondary ribs, which bifurcate into tertiary ribs adventrally of the middle of the flank. Rarely they split into 3 tertiary ribs. The subdivision points are not situated exactly at the same level. Solitary bifurcating secondaries occur here and there.

No measurements and no observations of the shape of the shell are possible on the second paratype (GSC loc. 93753; Ke 76/11/7-9) because of its poor preservation. In this specimen the number of bullae is considerably decreased (10 to 12 estimated) already at a shell diameter of approximately 100 mm. The last preserved whorl, which is septate to the end, has 5-6 bullae per half whorl.

None of the specimens studied exhibit any constrictions.

Affinities and differences. P. balkwilli is allied to *P. canadensis*. It differs principally in the more slender and relatively higher whorls which are almost discoidal. *P. balkwilli* may be a terminal form of the *P. canadensis* type.

The suture line of *P. balkwilli* is similar to that of *P. canadensis*, *P. tschekanovskii* and *P.* aff. *tschekanovskii* (Figures 47b, 48a, 49a), except for the elements situated on the umbilical shoulder and the umbilical wall. These parts of the suture are much more regularly shaped and more strongly denticulated in *P. balkwilli* than those of any of the other three forms and these distinctions appear to be taxonomically significant. The external suture of *P. balkwilli* matches particularly closely that of *P. canadensis* (Figure 49a) in its orientation, degree of denticulation, and distribution of lobes on the whorl's surface. However, A1 and A2 of *P. canadensis* lack the marked adventral inclination of their equivalents in the *P. balkwilli* suture. Furthermore, the third auxiliary and the sixth saddle of *P. canadensis* are smaller, less denticulated and less regularly shaped structures in comparison with their equivalents in *P. balkwilli*. Finally, the suture of *P. canadensis* differs in an occasional presence of a partly exposed fourth auxiliary lobe at its umbilical seam in the oralmost sutures known. The external suture of *Polyptychites* n. sp. A (Figure 48b) differs in its strongly widened lateral lobes and even stronger (relatively) narrowed first to third lateral saddles.

Age and correlation. P. balkwilli has the same stratigraphic range as *P. canadensis* (see there for further details).

Remarks about P. canadensis-P. balkwilli species group.

Representatives of the *P. canadensis-balkwilli* species group form the second group of huge *Polyptychites* confined to the high Boreal (or Arctic) regions. They are the largest known representatives of the genus, and have slender whorls throughout the ontogeny. They lack *Euryptychites*-like early or intermediate growth stages. The shallow and step-like umbilicus is also characteristic. It contrasts strongly with the more nearly funnel-like umbilicus of other species.

Another peculiarity of the species group consists in the small number of bullae and their shape. The bullae are very low, broad and pronouncedly comma-like on the umbilical wall. They become elevated only in the adult growth stage, while acquiring at the same time an approximately conical shape. The group — like the bulk of other representatives of *Polyptychites* — is characterized by the restriction of particularly prominent bullae to the adult growth stage. As happens commonly elsewhere in the genus, this development proceeds parallel with a weakening of the sculpture on the flanks, which begins already in the intermediate growth stages. The ribs persist longer on the ventral rounding of the whorl, and bend forward distinctly in the early and intermediate growth stages. The sculpture of still earlier growth stages was only observed in the holotype of *P. canadensis*, where it is fine and dense. It is inferred accordingly that the whole of the *canadensis-balkwilli* species group should be assigned to those *Polyptychites* in which the young forms are characterized by delicately and closely spaced sculpture.

The forward arching of ribs on the venter, which is especially well developed in the holotype of *P. canadensis*, as well as the tendency to have a slender whorl cross-section and approximately discoidal shells, resemble the morphological appearance of these features in *Dichotomites* and *Prodichotomites*. The same is true of the bundling habit of the holotype of *P. canadensis*, which resembles that of some *Prodichotomites* species, such as *P. hollwedensis* and *P. polytomus*. However, these similarities are a matter of convergent evolution, as other features of the species group evolve in the exactly opposite direction. In particular, the shells of the *canadensis-balkwilli* species group reach a size two to three times greater than that of the largest *Prodichotomites*- and *Dichotomites* species with the exception of *Prodichotomites grotriani* and an unnamed *Prodichotomites* mentioned in the chapter on NW German Polyptychitinae. These shells are relatively thicker than those of the thickest *Prodichotomites* species (their largest wth expressed as percentage of the shell diamter is 45 per cent as compared with 38 to 39 per cent in thick *Prodichotomites* species). The bullae of *Dichotomites* and *Prodichotomites* are regularly developed and evenly spaced to their oral end. The intermediate growth stages of *Prodichotomites* exhibit at least 17 but mostly still more bullae per whorl. In *Dichotomites*, this number comprises, as a rule, more than 20. The corresponding growth stages of the *canadensis-balkwilli* species group exhibit, in contrast, 10 to 12 bullae. Furthermore, the bullae of this species group change their shape from low swellings in youth to high conical structures in the adult growth stage.

The overall evaluation of the above data indicates that the *canadensis- balkwilli* species group remains essentially *Polyptychites*-like, even though it has developed some morphological features which resemble those of *Dichotomites* and *Prodichotomites*. Therefore, it cannot be placed in *Prodichotomites* but must be interpreted as an independent, somewhat older dead end offshoot of *Polyptychites* restricted to the Arctic basins.

Genus *Prodichotomites* Kemper 1971
(see p. 90 for discussion and generic diagnosis)

Prodichotomites aff. *hollwedensis* Kemper 1978

Pl. 45, fig. 2; Pl. 46, fig. 3; Pl. 49, figs. 3A-3C; Figure 50

1973	*Polyptychites (Dichotomites)* ex aff. *ascendens* Jeletzky, p. 68
1977	*Dichotomites (Prodichotomites) hollwedensis* Kemper, p. 4 (nomen nudum).
	(see p. 95 for the synonymy of European representatives of the species).

Material. One incomplete but otherwise relatively well preserved specimen from Amund Ringnes Island, N.W.T., GSC loc. 85023, GSC Cat. No. 77118.

Locus typicus. Amund Ringnes Island, Lat. 78°38'N; Long. 97°50'W. Exact location unknown.

Stratum typicum. Upper part of the Deer Bay Formation. Exact horizon unknown but presumed to correspond to some part of the fossiliferous beds 8-9 of Kemper (1977, Fig. 3) and to be derived from beds equivalent to the lower part of the Hollwedensis Zone and of the latest early Valanginian age (Kemper and Jeletzky, 1979, p. 13, Figure 9; this paper Figure 62).

Measurements (in mm).

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
GSC Cat. 77118	89	22(25)	31(35)	36(40)	-	38(?)

Description. Only a partly distorted fragment of the last whorl is preserved. It is evidently not septate any more and so should represent the living chamber. If so, the terminal shell diameter would be about 130 to 150 mm. The penultimate whorl seems to be slightly deformed also so that its real shape remains uncertain. As they are pre-

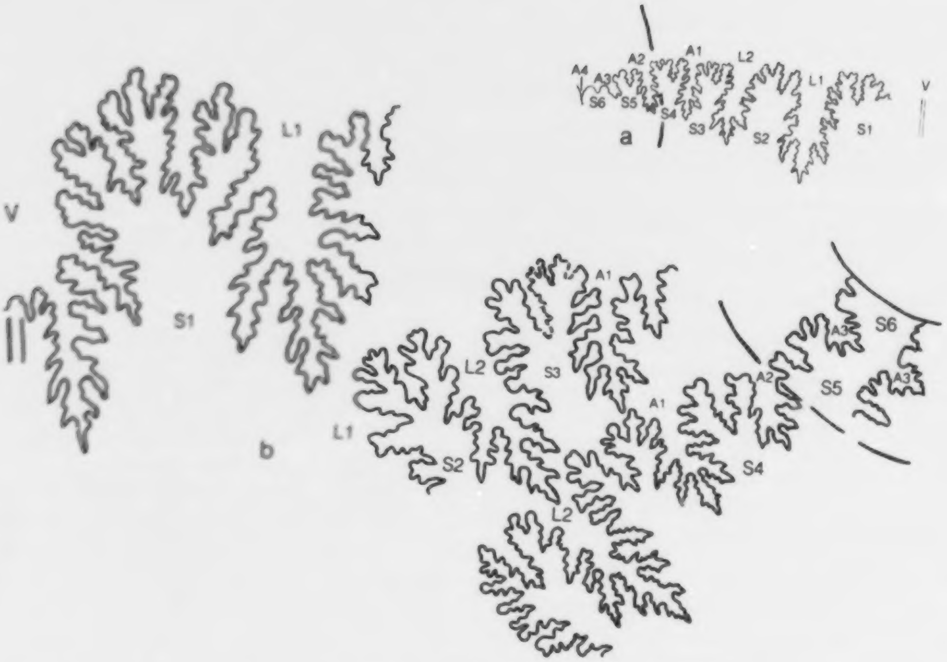


Figure 49. Adult external suture lines of the Canadian *Polyptychites* species. **a**. *P. canadensis* Kemper & Jeletzky 1979. Holotype, GSC Cat. 61755 (Pl. 30, fig. l; Pl. 31, figs. 1A, 1B). Incomplete (lacks the ventral lobe) early adult suture observed at the whorl diameter of 55 mm (approx.), x 1. **b**. *P. balkwilli* n. sp. Holotype, GSC Cat. 77117 (Pl. 44, fig. 4; Pl. 45, fig. 1). Three successive (incomplete but complementary) advanced? adult sutures observed at the whorl diameter of about 90 mm, x 1.

served, the whorls are somewhat broader than high and the flanks are only feebly convex. The ventral rounding has a somewhat narrow-arched appearance.

The umbilical shoulder forms a broad arch which grades into the low and at 50 to 60 degrees relatively gently inclined umbilical wall. The narrow to moderately wide umbilicus is accordingly shallow. About 77 per cent of the penultimate whorl is covered by the last whorl.

The adult external suture line is almost completely (i.e. except for the ventral lobe; Pl. 49, fig. 3B; Figure 50) exposed on the early part of the presumably adult penultimate whorl. This advanced polyptychitinid suture line has three auxiliary lobes in addition to two lateral lobes. Of these, the two lateral lobes and the first auxiliary lobe are situated on the flank while the second and third auxiliaries are situated on the umbilical wall. The second auxiliary is situated just below the umbilical shoulder so that all of the fourth lateral (i.e. A1/A2) saddle is situated on the adumbilicalmost part of the flank. The third auxiliary is situated just inside the inner third of the umbilical wall (Figure 50). The imaginary line connecting the tops of the saddles of the lateral part of the suture line is approximately straight and ascendant at 25 to 30 degrees while that connecting the tops of the saddles of its umbilical part is subradial to only slightly ascendant. The two parts meet at a very obtuse angle. All these features fall well within the previously described and illustrated (p. 95-99; Figures 38a-38c) range of morphological variation of adult external suture lines of the Northwest German representatives of *D. hollwedensis*. However, the Canadian suture differs from these in:

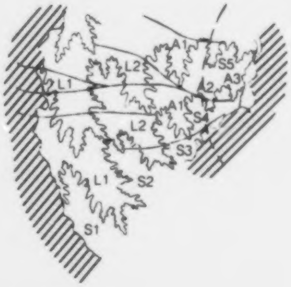


Figure 50. Advanced adult external suture lines of *Prodichotomites* aff. *hollwedensis* Kemper 1978. Specimen GSC Cat. 77118 (Pl. 45, fig. 2; Pl. 46, fig. 3; Pl. 49, fig. 3). Two incomplete sutures (lacking the ventral lobe) observed on the early part of adult penultimate whorl (Pl. 45, fig. 2; Pl. 46, fig. 3) at the shell diameter of about 93 mm, x 1.

1. Generally more shallow and less complex denticulation of all its elements;
2. A relatively sturdier and broader proportions of all its lobes;
3. A relatively much lesser width of all its saddles situated on the flank (i.e. of the E/L1, L1/L2 and L2/A1; compare Figure 50 with Figures 38a-38c); and
4. An irregularly bifid to very irregularly trifid (instead of the regularly to but rarely somewhat irregularly trifid) termination of the first auxiliary lobe. In this lobe, the largest, normally centrally situated and directly backward directed (e.g. Figures 38a-38c) terminal prong is pronouncedly deflected adventrally. The obliquely adventrally directed adventral prong is, at the same time, reduced in size and situated higher up the lobe's flank than the adumbilical prong (Pl. 45, fig.2; Pl. 46, fig. 3; Figure 50). This type of termination of the first lateral lobe was observed in at least six consecutive suture lines (Pl. 49, fig. 3B) and so could hardly be of a pathological origin. The same is, furthermore, true of the morphological features 1-3.

The combination of the distinctive morphological features 1-4 result in the adult external suture of the Canadian specimen being more similar to that of *Polyptychites hapkei* (e.g. of kv 284 and 344; Figures 33b; 36b) than to any variants of the equivalent external suture line of *D. hollwedensis* (Figures 38a-38c). However, the latter is still insufficiently known and so variable that it may conceivably include yet other morphologically conservative variants that would match closely the suture line of the Canadian specimen.

The penultimate whorl is ornamented by 19 delicate bullae, which split into two secondary ribs which then bifurcate at about the same level somewhat adventrally of the middle of the flank. Another bifurcating secondary rib with an equally high division point is simply intercalated between some of the bundles. The lower parts of the secondaries are somewhat indistinct, except at the earliest exposed part of the whorl, and this weakening of the ribbing on the lower flank increases gradually adorally. The secondary ribs form pronounced, forwardly convex bends on the ventral rounding (Pl. 49, fig. 3C). The gradual weakening of the ribbing ends in its disappearance on the last whorl in the zone situated between the bullae and the mid-flank. This results in a *Neocraspedites*-like appearance of that whorl. No constrictions were observed.

The bullae are slender, high and somewhat comma-like (bent forward) on the second and first before last whorls. Their extensions on the umbilical wall end only shortly before its seam. On the last whorl the bullae become somewhat more heavily built and, therefore, have a more typical appearance. On the last halfwhorl they are developed as flat, radial swellings, which are still comma-like on the umbilical wall where they extend to its seam. The number of the bullae decreases to 16-17 on the last (adult) whorl.

Affinities and differences. The evidently medium-sized shell, the regular distribution of the bullae, the slender whorls with but a minor increase of their height/width ratios are the features which in combination differentiate this specimen from all others known from the Sverdrup Basin. These features are, at the same time, diagnostic of those primitive *Prodichotomites* forms of which the variable species *Prodichotomites hollwedensis* is representative. The Canadian specimen belongs to the relatively narrowly umbilicated and regularly ribbed variants of this species group.

Among the NW German representatives of *P. hollwedensis*, the specimen reproduced in Pl. 27, fig. 2; Pl. 28; fig. 4 resembles most closely the Canadian specimen. Other examples have a wider and more step-like umbilicus combined with a denser sculpture (Pl. 16, fig. 1A-1C). However, this species has an obvious tendency, at least on the early to intermediate growth stages, to develop rib bundles consisting of three more or less regularly bifurcating secondary ribs. The reader is referred to Kemper's (1978) paper for further details and figures of *P. hollwedensis*.

Because of its slightly different ornament and whorl shape and the differences in its adult external suture line, the Canadian specimen cannot be assigned to *P. hollwedensis* with certainty. However, the two forms are obviously very closely allied and could conceivably be but morphologically extreme variants of the same highly variable species. Alternatively, the Canadian specimen could be a slightly older, conservative form of *P. hollwedensis* yet to be found in Northwest Germany. Therefore, it is being described herein in the open nomenclature as *P.* aff. *hollwedensis* Kemper 1971 instead of being treated either as a formally named, vicarious subspecies or as an independent, vicarious species of the *P. hollwedensis* species group.

The distinctions of our form from *Polyptychites* ex gr. *canadensis — balkwilli* are discussed in their descriptions. It is impossible to confuse *P.* aff. *hollwedensis* with any other Polyptychitinae species occurring in the Sverdrup Basin.

Age and correlation. The specimen was collected by geologists of Mobil Oil Co. of Canada, Ltd. from GSC loc. 85023. No other ammonites were found at that fossil locality and its stratigraphic position within the upper Deer Bay Formation is unknown. However, it is assumed to represent beds equivalent to Beds 7-9 of Kemper's (1977, p. 3, Fig. 3; this paper, Figure 62) Section 74/11. If so, the specimen is derived either from the lower/upper Valanginian boundary beds or from basal upper Valanginian beds.

Genus *Siberiptychites* Kemper and Jeletzky 1977

Synonymy

1977	*Siberiptychites* subgenus novum Kemper and Jeletzky *in* Kemper, p. 3.
1981	*Siberiptychites* Klimova, p. 74, 80.

Type species. *Ammonites polyptychus* var. *stubendorffi*

Schmidt 1872 as re-interpreted by Pavlow (1914, p. 29) and the writers (see Kemper 1977, p. 3 and p. 141 of this paper).

Derivation of name. The name *Siberiptychites* commemorates the prevalent occurrence of the representatives of the genus in high Boreal (or so-called Arctic) basins of Northern Siberia while stressing its inferred affinities with the genus *Polyptychites* s. str., the representatives of which are largely restricted to the marginal Boreal (or so-called Subarctic) basins.

Diagnosis. Polyptychitinids characterized by: 1. The presence of three to four auxiliary lobes; 2. The presence of frequent constrictions; 3. A greater density of primary ribs than in *Polyptychites* (22 to 30 on early whorls and 20 to 26 on outer whorls); 4. A complex sequence of whorl shapes beginning with a globular or/and an *Euryptychites*-like, changing into a *Polyptychites rectangulatus*-like, and ending with a *Polyptychites*-or *Euryptychites*-like; and 5. A complex sequence of rib patterns starting with predominantly trichotomous *Bodylevskites*-like bundles, followed by simple dichotomous bundles, then by predominantly trivirgatitpartitous bundles, and then by predominantly quadripartitious bundles. Umbilical bullae appear in the last two patterns. The sequence ends with a *Polyptychites*-like weakening or prevalent loss of ornamentation.

Type area. Central part of North Siberia (Anabar-Khatanga Basin).

Stratigraphy and age. According to the latest data available (e.g. Klimova, 1978, p. 74, 81; Gol'bert et al., 1981, p. 56-59, Tables 4, 14), the North Siberian *Polyptychites*- and *Euryptychites*-like ammonites here assigned to *Siberiptychites* are restricted to the regional lower Valanginian zones of *Temnoptychites syzranicus* and *Polyptychites michalskii* (see Figure 62). According to these workers, these two zones represent the whole lower Valanginian. This view is now shared by Jeletzky (1984) who has abandoned his earlier ideas about the basal Valanginian age of the next older *Tollia mesezhnikowi* (= *Tollia tolli*) Zone (compare Jeletzky, 1973, Fig. 3; 1979, p. 56-58, Text-fig. 8).

Judging by the somewhat scanty data available, the earliest *Siberiptychites* represented by *S.* (*S.*) *stubendorffi* only, appear already in the *Temnoptychites simplicissimus* Subzone (= *Neotollia klimovskiensis* Zone of Saks and Shulgina, 1969; 1974, p. 146, Corr. Table) that represents the basal Valanginian (Figure 62). In this subzone *S.* (*S.*) *stubendorffi* is associated with *Bodylevskites* spp. and the first representatives of *Astieriptychites* (Gol'bert et al., 1981, p. 56, Table 4). So far as is known, all other representatives of the subgenus *Siberiptychites* (mostly listed as "*Polyptychites*" ex gr. *stubendorffi* and "*Polyptychites*" ex gr. *middendorffi*) and *Pseudoeuryptychites* (always listed as "*Euryptychites*" spp.) first appear in the next younger *Temnoptychites syzranicus* Subzone (Figure 62).

All modern Siberian workers agree that the genus *Siberiptychites* does range up into the upper part of the *Polyptychites michalskii* Zone, which contains numerous *Polyptychites* ex gr. *keyserlingi* (e.g. *P.* cf. *keyserlingi* and *P.* aff. *keyserlingi* of Gol'bert et al., 1981, p. 59, Table 4). They also agree that neither *Siberiptychites* s. str. (i.e. their "*Polyptychites*" ex gr. *stubendorffi-middendorffi*) nor *Pseudoeuryptychites* (i.e. their "*Euryptychites*" spp.) range up into the early late Valanginian "*Dichotomites ramulosus*" Zone (= *Dichotomites* spp. Zone of Saks et al., 1963; Saks and Shulgina, 1974, p. 146, Corr. Table). The opposite opinion of Bodylevsky (1968, p. 310 and in Berg et al., 1949, p. 204) and Krimgolts et al. (1953, p. 82), who have assigned a late Valanginian age to all beds containing *Siberiptychites* s. str. and *Pseudoeuryptychites* in the Anabar-Khatanga region is refuted by the more recent research beginning with that of Saks et al. (1963, p. 178-181, Table 8).

The published data available do not make clear the stratigraphic position of beds corresponding to the *Polyptychites tschekanovskii* Beds of the Sverdrup Basin in the sequence of North Siberian fossil zones. Neither Klimova (1978, 1981) nor Gol'bert et al. (1981) list this important species among the diagnostic fossils of either the *Polyptychites michalskii* or the *Dichotomites ramulosus* Zones. However, it seems likely that the Canadian *Polyptychites tschekanovskii* Beds (Kemper and Jeletzky, 1979, p. 13, Fig. 9) form part of the *Polyptychites michalskii* Zone as defined by these workers. According to Gol'bert et al. (1981, p. 59, 63), *Polyptychites canadensis* Kemper and Jeletzky, restricted to these beds in the Sverdrup Basin, is an index fossil of the regional *Polyptychites michalskii* Zone. If so, the genus *Siberiptychites* probably ranges up into the equivalents of the *Polyptychites tschekanovskii* Beds in Northern Siberia.

As already recognized by Kemper (1975, 1977) and Jeletzky (1979, p. 56-58, Text fig. 8), the time range of *Siberiptychites* (*Siberiptychites*) ex gr. *stubendorffi* and *S.* (*Pseudoeuryptychites*) *middendorffi* in the Sverdrup Basin is much more restricted than their time range in Northern Siberia. Furthermore, as demonstrated later (pp. 151-152, and 176-179), the same is true of all other Canadian representatives of the genus, which are confined to narrow sequence of beds in the upper Deer Bay Formation roughly corresponding to the middle part of the North Siberian *Polyptychites michalskii* Zone. They are not known to range either down into the regional *Thorsteinssonoceras ellesmerense* Beds corresponding to the lower part of that zone or up into the regional *Polyptychites tschekanovskii* Beds corresponding to its uppermost part. However, they are inferred to range up into the regional beds containing *Polyptychites keyserlingi* that are assumed to underlie immediately the *Polyptychites tschekanovskii* Beds (Figure 62).

The probable causes of these discrepant time ranges of the genus *Siberiptychites* are also discussed below (pp. 151-152).

Geographical range. Northern Siberia, Arctic Canada (Sverdrup Basin), European Arctic (East Greenland, Spitsbergen).

Discussion. The morphological and geographical peculiarity of *Polyptychites stubendorffi* (Schmidt) was recognized already by Pavlow (1914, p. 28, 29) who segregated this species together with other closely related North Siberian forms (e.g. *P. middendorffi* Pavlow) as *Polyptychites* of the group of *Polyptychites stubendorffi* (Schmidt). The geographical isolation of this species group and its restriction to Arctic regions of Eurasia and North America was confirmed by all subsequent workers, including the writers. Taken together with several rather, although not always hundred percent, constant morphological distinctions from all Northwest German, English and Russian *Polyptychites* forms with which the authors are familiar, this geographical isolation of "*Polyptychites*" ex gr. *stubendorffi* clearly indicates its phylogenetically isolated position. The writers decided accordingly to treat this Arctic offshoot of the main *Polyptychites* stem as a new subgenus and named it *Siberiptychites* (Kemper and Jeletzky, *in* Kemper, 1977, p. 3). It was elevated to full generic rank by Klimova (1981, p. 74, 81), who has discovered additional morphological distinctions from *Polyptychites* s. str., and, following her, by Jeletzky (1986). The writers follow this example, particularly because of the somewhat earlier discovery of the genus *Bodylevskites* (Klimova, 1978) in Northern Siberia that is interpreted herein as the immediate ancestor of *Siberiptychites* (see p. 20, 21 for further details). *Siberiptychites* differs from the predominantly but not exclusively temperate to subarctic genus *Polyptychites* in the following morphological features:

1. The greater number and a different arrangement of auxiliary lobes as compared with the contemporary or earlier *Polyptychites*. As noted earlier (p. 21, 22), the adult external suture line of *Siberiptychites* has at least three auxiliary lobes. Of these, either only the second and the third (in *Siberiptychites* s. str.) or all three (in *Pseudoeuryptychites*) are situated on the umbilical wall. The fourth auxiliary lobe may be visible at or near the umbilical seam in some *Siberiptychites* s. str. in which the two lateral and the first and second auxiliary lobes are situated on the shell's flank. In contrast, the external suture lines of most better known, contemporary or earlier representatives of *Polyptychites* including such homoeomorphs of *Siberiptychites* as *P. ramulicosta* (see Pavlow, in Pavlow and Lamplugh, 1892, Pl. XV, fig. 6A), have only two auxiliary lobes (see p. 11, 12 for further details). The third auxiliary lobe mostly appears only in advanced representatives of *Polyptychites* that occur in younger beds than the bulk of *Siberiptychites* and are unrelated to any of its representatives, being direct descendants of earlier Northwest German *Polyptychites* forms (see p. 68-69).

2. The characteristic presence of constrictions which average one per whorl in the material studied and are more common on the inner whorls. However, as pointed out by Pavlow (1914, p. 32) and confirmed by the writers, the constrictions may be either very feebly developed or even completely absent in some rare representatives of *Siberiptychites*. In contrast, such constrictions are totally unknown in *Polyptychites* and related European polyptychitinid genera (e.g. *Peregrinoceras* s. Casey 1973, *Paratollia*, *Praepolyptychites*, *Prodichotomites* and *Dichotomites*).

3. The presence of a complex sequence of whorl shapes that is unlike that of *Polyptychites*, other Northwest European polyptychitinids, and *Astieriptychites*. Some details of this sequence, particularly the details of its variation from one *Siberiptychites* s. str. species to another and from the *Siberiptychites* s. str. to *Pseudoeuryptychites*, remain insufficiently understood but its general validity for the genus *Siberiptychites* is sufficiently well established.

Klimova (1981, p. 75, 77; Figures 2-1 to 2-5 incl.) was apparently the first to describe some of these whorl shapes on the example of *S.* (*S.*) *stubendorffi* which she considered to be the only firmly established representative of the genus *Siberiptychites* (Klimova, ibid., p. 80, 81). Later it was shown by Jeletzky (1986, p. 352, 355) that this sequence of whorl shapes also occurs in the type species of the subgenus *Pseudoeuryptychites* and so is diagnostic of the entire genus in its expanded interpretation. Jeletzky (ibid., p. 355) has also named the first *Euryptychites*-like, the intermediate *Polyptychites rectangulatus*-like, and the adult *Euryptychites*-like growth stages on the example of *S.* (*Pseudoeuryptychites*) *pavlovi*.

The shape and proportions of the earliest few whorls of *Siberiptychites* are still poorly known but appear to vary markedly in the few forms where they are known. In one of these — the *S.* (*S.*) *stubendorffi* — the earliest three whorls are *Euryptychites*-like shaped and proportioned, except for the well rounded umbilical shoulder (Klimova, 1981, p. 75, 77, Pl. IX, fig. 1a-1c; Figures 2-1, 2-2, 2-3). This apparently uniformly shaped and proportioned initial growth stage was designated "the first *Euryptychites*-like growth stage of *Siberiptychites*" by Jeletzky (1986, p. 355). The shape and proportions of the earliest one to two (possibly up to three) whorls of *S.* (*Pseudoeuryptychites*) *middendorffi* originally described in this paper (p. 163, Figure 54d) differ in an about equidimentional, approximately globular shape and in the absence of umbilical and ventral shoulders. This distinctive *globular growth stage* lasts until the shell diameters ranging from about 3.5 to 5 (or possibly 6) mm and then grades into the typical first *Euryptychites*-like growth stage (height/width ratio of 55 to 58 per cent), which only differs from that of *S.* (*S.*) *stubendorffi* in its larger size and different, more advanced ontogenetic position. In *S.* (*P.*) *middendorffi* this first *Euryptychites*-like growth stage lasts at least through the next one to one and a half whorls (and possibly more in the var. *incrassata*) and ends at the shell diameters ranging from about 10 to about 20 mm. The only other known example of the first *Euryptychites*-like growth stage is its terminal part exposed in *Siberiptychites* (*Pseudoeuryptychites*) *pavlovi* (see p. 175). Judging by the dimensions of this cross-section, it represents the shell diameter of at least 12 mm and ends at the same growth stage as does that of *S.* (*P.*) *middendorffi*.

The *S.* (*S.*) *stubendorffi*-like variant of the first *Euryptychites*-like growth stage is present already in *Bodylevskites* (Klimova, 1978, p. 54, Figures 1-1 to 1-5, 2-1), which occurs in slightly older rocks than and appears to be directly ancestral to *Siberiptychites* s. str. (see p. 20, 21). Therefore, this initial ontogenetic growth stage appears to be a new, presumably adaptive feature that arose in this otherwise slender and discoidal genus. The stage must have been inherited unchanged by the oldest and most primitive *Siberiptychites* (*Siberiptychites*) ex *gr. stubendorffi* but was displaced adorally in the ontogeny of the descendant *S.* (*Pseudoeuryptychites*) *middendorffi* which is the most primitive member of the subgenus *Pseudoeuryptychites*. The first *Euryptychites*-like growth stage is known to end similarly late in *S.* (*P.*) *pavlovi*. Therefore, it seems likely that the *S.* (*P.*) *middendorffi*-like variant of this growth stage and the initial, globular growth stage are equally characteristic of the entire subgenus *Pseudoeuryptychites*. Though scant and incomplete, these data suggest that the oralward displacement of the first *Euryptychites*-like growth stage in the phylogeny of the genus *Siberiptychites* and the appearance of the initial globular growth stage in its former position in the more advanced representatives of this genus followed a prophetic (or proterogenetic) evolutionary mode.

The first *Euryptychites*-like growth stage was not observed in any suitably preserved Northwest German *Polyptychites* species (e.g. this paper, Pl. 4, figs. 4, 6B; Pl. 5, fig. 3B; Pl. 11, fig. 2B: Pl. 12, fig. 3A-3C; Koenen, 1902, Pl. 55, figs. 5b, 11b, 12b). Nor is it known to be present in any suitably preserved English *Polyptychites* (e.g. Danford, 1906, Pl. XI, figs. 2a, 3a, 5a). All these early whorls are characterized by a considerably more slender and high, *P. ascendens*- to *P. keyserlingi*-like shape that seems to persist right through and to connect their initial, smooth to only faintly striated growth stage with the typically *Polyptychites*-like semiadult and adult whorls. This ontogeny is also known to occur in the *P. keyserlingi* species group which is the core of the Northwest European *Polyptychites*. Though the ontogeny of some Northwest European *Polyptychites* species remains poorly known or unknown, the data available are strongly suggestive of the absence of the first *Euryptychites*-like growth stage in its ontogeny.

An early growth stage closely resembling the first *Euryptychites*-growth stage of the *Siberiptychites* is present in the high Boreal *Polyptychites tschekanovskii* species group (see p. 123, 125) and in the Central Russian *P. michalskii-P. rectangulatus* species group (Bogoslovsky, 1902, p. 49, Pl. XV, fig. 6b; Pl. XVI, figs. 1b, 5b). However, this is likely to be a homoeomorph development because of a younger age and an evolutionary and geographical isolation of these species groups which may have to be separated generically from the Northwest European *Polyptychites* stock in the future.

The first *Euryptychites*-like growth stage grades rapidly into the next older growth stage characterized by a moderately sturdy to moderately slender (its height/width ratio varies from 80 to 105 per cent), rounded-trapezoidal to rounded-rectangular cross-section, in which the but slightly convex flanks are delimited by distinct shoulders from the feebly convex umbilical wall and the slightly to moderately arched venter. The overall shape of this growth stage may be similar either to the early, but not the earliest, whorls of *Bodylevskites* (Klimova, 1978, Pl. 1, fig. 2b; Pl. 2, fig. 2b) or to the intermediate and advanced whorls of *Polyptychites rectangulatus* (Bogoslovsky, 1902, Pl. XVI, figs. 2a, 5b) depending on the degree of convergence (or lack thereof) of the flanks, the width of the venter, and the degree of its arching. This **Polyptychites rectangulatus-like growth stage** (Jeletzky, 1986, p. 355) is now known to occur in the same ontogenetic position in *S.* (*S.*) *stubendorffi*, *S.* (*S.*) n. sp. aff. *stubendorffi*, *S.* (*S.*) *fascicostatus*, *S.* (*Pseudoeuryptychites*) *middendorffi*, and *S.* (*P.*) *pavlovi* and so is diagnostic of the entire genus *Siberiptychites*. Like the preceding first *Euryptychites*-like growth stage, this stage must have been inherited essentially unchanged by *S.* (*S.*) *stubendorffi* from the directly ancestral *Bodylevskites* (compare Klimova, 1978, Pl. 1, fig. 2b; Pl. 2, fig. 2b with Pavlow, 1914, Pl. V, figs. 6, 7 and Klimova, 1981, Pl. IX, figs. 2b, 3a). However, it is considerably more sturdy and essentially *Polyptychites rectangulatus*-like shaped in the evolutionarily more advanced *S.* (*S.*) n. sp. aff. *stubendorffi* (Pl. 42, fig. 1, Pl. 63, fig. 2C; Figure 54c), *S.* (*S.*) *fascicostatus* (Pl. 61, fig. 1B), *S.* (*Pseudoeuryptychites*) *middendorffi* (Pl. 34, fig. 3E), and *S.* (*P.*) *pavlovi* (Pavlow, 1914, p. 37, Pl. IX, fig. 2c). The **Polyptychites rectangulatus**-like growth stage extends over at least three intermediate whorls in *S.* (*P.*) *middendorffi*; (see p. 163, 164). However, its exact duration is mostly uncertain and may considerably exceed this estimate in *S.* (*S.*) *stubendorffi* (Pavlow, 1914, Pl. V, figs. 6, 7) and some other forms.

The character of termination of the *Polyptychites rectangulatus*-like growth stage and the subsequent ontogeny of the whorl shape and proportions vary strongly within *Siberiptychites*. In the more slender representatives of *Siberiptychites* s. str., such as the slender variant of *S.* (*S.*) *stubendorffi* (Pl. 36, fig. 1C; Figure 54b; Klimova, 1981, Pl. IX, figs. 4a, 5), *S.* (*S.*) n. sp. aff. *stubendorffi* (Pl. 37, fig. 1B; Pl. 42, fig. 1), and *S.* (*S.*) *fascicostatus* (Pl. 35, fig. 2B; Pl. 61, fig. 1B), the end of this stage is ill-defined as the whorl shape changes relatively little, if at all, through the remainder of their known ontogeny. This includes the early part of the adult last whorl wherever it is preserved. In these forms all whorls succeeding the *Polyptychites rectangulatus* growth stage are either *Polyptychites keyserlingi*- or *Polyptychites beani*-, or even *Polyptychites ascendens*-like. Therefore, neither the shape of the *Polyptychites rectangulatus*-like whorls nor that of the successive whorls differ materially from that of the equivalent whorls of the Northwest European *Polyptychites*. It is because of this similarity that *Siberiptychites* ex gr. *stubendorffi* have been originally assigned to the *Polyptychites* and kept in that genus until recently.

The situation is different in the morphologically and (mostly) phylogenetically more advanced sturdy variant of *S.* (*S.*) *stubendorffi* (Pl. 44, fig. 1A; Figure 54a) and in all better known *Pseudoeuryptychites* forms (e.g. *S. (P.) middendorffi*; Pl. 36, fig. 2B; Pl. 40, figs. 2A, 2B, *S.* (*P.*) *pavlovi*; Pavlow, 1914, Pl. IX, fig. 2c or *S. (P.)* n. sp. A; Pl. 67, figs. 2A, 2B; Figure 54f) where the relatively shortened (see Jeletzky, 1986, p. 355; this paper, p. 164, 175, 179) *Polyptychites rectangulatus*-like stage is followed by the **second Euryptychites-like growth stage**, which only differs from the first one in its much larger size, the ontogenetically terminal position, and the prevalent (i.e. except in the sturdy variant of *S.* (*S.*) *stubendorffi* and in *S.* (*P.*) *middendorffi*) presence of an acute umbilical shoulder. In these morphologically and mostly evolutionarily advanced forms this growth stage develops out of the *Polyptychites rectangulatus* growth stage either directly and rapidly or via an intermediate *Polyptychites keyserlingi*- or *P. hapkei*-like whorl shape; it lasts through their oralmost three to four whorls, including the early part of the adult last whorl (i.e. the adult living chamber), and is inferred to last to the oral end of this whorl. This recurrence of an *Euryptychites*-like whorl shape at the end of the ontogenetic development appears to be a unique phenomenon in the entire subfamily Polyptychitinae.

This restriction of the *Polyptychites rectangulatus*-like growth stage to a few intermediate whorls coupled with the addition of the new terminal *Euryptychites*-like growth stage appears to represent an abbreviated recapitulation of the much more extensive, commonly terminal ontogenetic stage in the ancestral *Bodylevskites* and *S.* (*S.*) ex gr. *stubendorffi* combined with the addition of a new, presumably adaptive growth stage. This newly added second *Euryptychites*-like growth stage can be interpreted as an adaptation to a less active, nectobentonic mode of life of these *Cadoceras*-like adults of advanced *Siberiptychites*. The evolution of these advanced to adult growth stages of the genus must have followed a palingenetic mode.

4. The presence of a complex sequence of rib patterns that is unlike that of *Polyptychites* and other Northwest European polyptychitinids and is uniquely complex for the entire subfamily. This sequence was originally described, in part, by Klimova (1981) on the example of *S.* (*S.*) *stubendorffi*. Later it was shown by Jeletzky (1986) to be present in the subgenus *Pseudoeuryptychites*. It is now known to be present, albeit with some modifications, in *S.* (*S.*) *stubendorffi*, *S.* (*S.*) n. sp. aff. *stubendorffi*, *S.* (*S.*) *fascicostatus*, *S.* (*P.*) *middendorffi*, and *S.* (*P.*) *pavlovi* and is considered to be diagnostic of the entire genus *Siberiptychites*.

   The initial, essentially smooth (except for the characteristic constrictions; Pl. 38, figs. 3A, 3B; Pl. 40, fig. 3) sculptural phase ends in the appearance of threadlike striae and siphonal riblets on the third to fourth earliest whorls (Klimova, 1981, p. 75, 77; this paper, p. 143, 165; Pl. 38, figs. 3A, 3B). It was designated the stage of appearance of ribs by Klimova (l. cit.) but is designated herein the **smooth sculptural stage.** It is followed gradationally by the second sculptural stage ornamented predominantly by an alternation of fine, very closely spaced and pronouncedly flexuous trivirgatitpartitous and trifasciculate rib bundles (Pavlow, 1914, Pl. V, figs. 6, 7; this paper, Pl. 39, figs. 3F, 3G; Figure 51a). The supplementary ribs are strongly inclined forward and form prominent, forward convex loops on the venter. The sculpture is rather variable in details in different *Siberiptychites* species and may include subordinate dichotomous, quadrivirgatitpartitous, quadrifasciculate, and bidichotomous rib bundles and some intercalated single ribs. However, it is always rather similar to the early sculptural stage of *Astieriptychites* (e.g. Pl. 57, figs. 4D, 4E, 4G) and *Bodylevskites* (Klimova, 1978, Pl. 1, figs. 1, 1a, 4, 5, 5a, 6; Pl. 2, figs. 1, 1a, 2, 2a, 2b). This sculptural stage was named the stage of stabilization of rib bundles by Klimova (1981, p. 77; Pl. IX, figs. 2, 3) but it is designated herein the **Bodylevskites-like sculptural stage.** It begins on the fourth to fifth whorl from the protoconch and extends to the shell diameter of about 20 to 30 mm. It differs markedly from the earliest ornamented growth stage of *Polyptychites* (e.g. Pavlow & Lamplugh, 1892, Pl. VIII, figs. 10a, 11a; Pl. XV, fig. 5a; Bogoslovsky, 1902, Pl. XIV, fig. 1a; Pl. XV, figs. 2a, 3a, 5a; Pl. XVI, fig. 4a) which is dominated by much coarser and less flexuous to almost straight (stiff), roundtopped trivirgatitpartitous rib bundles with some intercalated dichotomous bundles. Their supplementary ribs are either subradially oriented or but slightly inclined forward and cross the venter transversally. Such sculptural stage is either unknown or poorly developed in *Siberiptychites* (e.g. in *S. (S.) stubendorffi*, see its description and in Klimova, 1981, p. 77, 78; Pl. IX, figs. 3, 4) or appears at later growth stages (e.g. in *S. (P.) middendorffi*; see Pl. 39, figs. 3A, 3B).

   According to Klimova (1981, p. 78, Pl. IX, figs. 4, 5), the *Bodylevskites*-like sculptural stage is followed by a "stage of regularized rib bundles" which is described as follows (Jeletzky's translation from Russian):

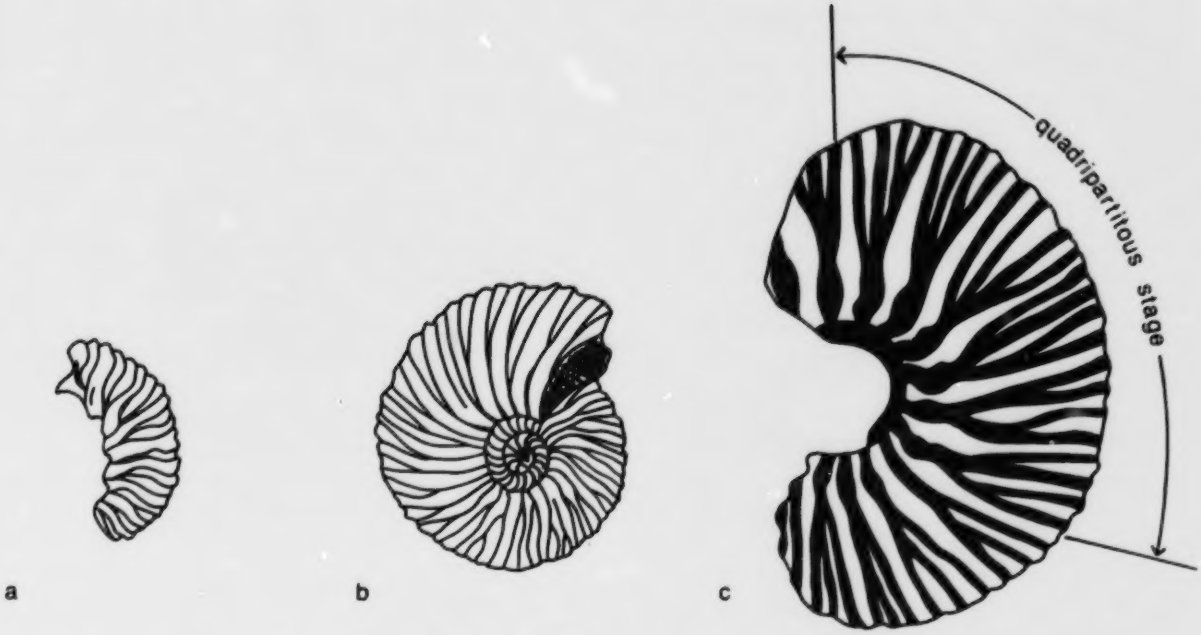


Figure 51. Principal sculptural stages of the genus *Siberiptychites*. **a**. *Bodylevskites*-like sculptural stage and the early part of simple dichotomous stage; based on the early whorl of the specimen GSC Cat. 17251. **b**. The late part of simple dichotomous stage and the early part of the predominantly trivirgatitparitious stage; based on the specimen GSC Cat. 77100. **c**. The terminal part of the predominantly trivirgatitpartitous stage and the predominantly quadripartitious stage; based on the last whorl of the specimen GSC Cat. 17251. All figures x 1 (approximately).

"The stage of regularized bundles is the third sculptural stage in the ontogeny of the here described form (i.e. its eighth whorl and the beginning of ninth whorl) (see Pl. IX, figs. 4, 6). The short elevated umbilical (i.e. primary; translator's remark) ribs begin in the upper half of the umbilical wall. They subdivide into two ribs. These siphonal (i.e. secondary; translator's remark) ribs subdivide in their turn. Both ribs of the original dichotomous bundle can subdivide producing a bidichotomous bundle. Alternatively, only one of them, usually the posterior, may bifurcate. The latter process results in the formation of either polyptychous (in the interpretation of most Soviet workers that equals the trivirgatitpartitous bundles of this paper; translator's remark) or virgatotomous bundles. The bundles consisting of four branches predominate. The triple polyptychous bundles are considerably more rare. The bundles consisting of five branches are also rare; they arise when the anterior rib of a bundle bifurcates while the posterior rib trifurcates."

This generalized description of "the stage of regularized bundles" which is claimed to last till adulthood of *S.* (*S.*) *stubendorffi*, does not agree with the sculpture observed on the advanced to adult whorls (i.e. on those immediately following the whorls ornamented by *Bodylevskites*-like rib bundles) of the Canadian *Siberiptychites*. Nor does it agree with the sculpture visible on equivalent whorls of previously published North Siberian *Siberiptychites*, except for the specimen of *S.* (*S.*) *stubendorffi* described and figured by Klimova (l. cit.). The authors' study of the presently known *Siberiptychites* species necessitates the replacement of Klimova's (1. cit.) "stage or regularized bundles" by three well defined sculptural stages, which are designated (from the earliest to the latest): the predominantly simply dichotomous (Figures 51a and 51b); the predominantly trivirgatitpartitous (Figures 51b and 51c), and the predominantly quadripartitious (Figure 51c) which were observed in this sequence in *S.* (*S.*) *stubendorffi*, *S.* (*S.*) n. sp. aff. *stubendorffi*, *S.* (*S.*) *fascicostatus* n. sp., *S.* (*Pseudoeuryptychites*) *middendorffi* and *S.* (*P.*) n. sp. indet. A (see their descriptions and illustrations for further details) and so are diagnostic of the genus as a whole.

The **predominantly dichotomous sculptural stage** is characterized by the prevalence of simple dichotomous rib bundles, which are mostly intercalated with subordinate trivirgatitpartitous and trifasciculate bundles. Rare intercalated single ribs with or without primaries may also be present.

The nonbullate primary ribs are fine, closely spaced, and high; they extend from the umbilical wall onto the lower one-third to one-half of the flank before bifurcating. The morphologically similar secondary ribs are approximately straight but inclined forward. There are 60 to 70 secondaries per whorl. The stage begins at the shell diameters ranging between 25 and 30 mm, extends over one to ?one and a half whorls and ends at the shell diameters ranging between 32 to 39 mm. The predominantly dichotomous sculptural stage occurs in *S.* (*S.*) *stubendorffi*, *S.* (*S.*) n. sp. aff. *stubendorffi*, *S.* (*S.*) *fascicostatus*, *S.* (*Pseudoeuryptychites*) *middendorffi* and *S.* (*P.*) n. sp. indet. A. but was not recognized by Klimova (1981, p. 77, 78) in the shell of *S.* (*S.*) *stubendorffi* taken apart by her. However, the constant presence of this sculptural stage in all above mentioned *Siberiptychites* s. str. and *Pseudoeuryptychites* forms, including *S.* (*S.*) *stubendorffi*, suggests that this specimen either is an aberration or its predominantly dichotomous stage was overlooked by Klimova (l. cit.). This stage could have been present in its unfigured interval between the shell diameters of 32 and 45 mm, as the preceding and the following shell segments are ornamented respectively by the *Bodylevskites*-like and the quadripartitous rib bundles.

The predominantly dichotomous sculptural stage is followed immediately and gradationally by the **predominantly trivirgatitipartious sculptural stage** which is characterized by an almost exclusive to prevalent presence of trivirgatitpartitous rib bundles but is rather variable otherwise. It may include a considerable to minor ratios of simple dichotomous (in the early phase of the stage only), quadrivirgatitpartitous, bidichotomous, and fasciculate rib bundles. The *ramulicosta*-like trivirgatitpartitous bundles where the anterior secondary birfurcates again are exceptionally rare (e.g. Pl. 38, fig. 3A; Pl. 36, fig. 1A). Other variable features of this stage are: the relative degree of coarseness and density of the primary and secondary ribs, the length of primaries and the level of their bifurcation, the degree of inclination and flexuosity of primaries and supplementaries on the umbilical shoulder and flank, the presence or absence of a forward arching of supplementaries on the venter, and an earlier or later transformation of nonbullate, thin, and relatively long primaries (similar to those of the preceding predominantly dichotomous stage) first into relatively shortened, but only slightly thickened (i.e. slightly bullate) primaries and then into the strongly shortened regular bullae. The morphology of all these features and the timing of their appearance or disappearance within the trivirgatitpartitous stage varies strongly from one *Siberiptychites* species to another and within at least some of these species. These features may even vary on the opposite flanks of the same specimen. Further details are provided in descriptions of individual species. The trivirgatitpartitous sculptural stage begins at different shell sizes and lasts unequally long in different *Siberiptychites* species. In *S.* (*S.*) *stubendorffi* where this stage is restricted to the second and/or last penultimate whorls and extends over one to one and a half whorls, it begins at the shell diameters from 45 to 55 mm and ends at those from 85 to 95 mm. However, in *S.* (*P.*) *middendorffi*, where this stage begins at the shell diameters ranging between 49 to 55 mm and ends at those from 63 to 66 mm and extends over one and a half to two whorls, it is markedly displaced to the earlier ontogenetic stages and ends within either the fourth or the third penultimate whorl. In *S.* (*S.*) *fascicostatus*, finally, this stage begins at the whorl diameter of 36 mm and ends at that of about 51 mm.

As pointed out in the description of *S.* (*S.*) *stubendorffi*, the trivirgatitpartitious sculptural stage is well developed in its previously published North Siberian and East Greenland representatives. However, like the preceding predominantly dichotomous stage, it was not recognized as such by Klimova (1981, Pl. IX, figs. 4, 6) and is not discernible in her photographs. It is not known whether Klimova's (l. cit.) specimen is anomalous or its trivirgatitpartitious stage was overlooked by her and is actually present within the unfigured interval confined between the shell diameters of 32 and 45 mm.

The trivirgatitpartitious stage grades oralward into the **predominantly quadripartitous sculptural stage** (Figure 51c) which is characterized by the prevalence of several kinds of quadripartitious rib bundles (i.e. bidichotomous, quadrivirgatitpartitous, quasibidichotomous, quadrifasciculate, and quasiquadrifasciculate) combined with a strong decrease to almost total disappearance of trivirgatitpartitous rib bundles and a markedly bullate appearance of the strongly shortened primary ribs. True polyptychous and trifasciculate rib bundles may be common and even prominent in some variants of the quadripartitous sculptural stage. This stage is even more variable morphologically than the preceding trivirgatitpartitious stage. Even the ratio of the principal types of its quadripartitious bundles vary strongly from one species to another and even infraspecifically. For example, in *S.* (*S.*) *fascicostatus* and *S.* (*S.*) n. sp. aff. *stubendorffi* this stage differs in the prevalence of quadrifasciculate bundles which are associated mostly with a considerable ratio of trifasciculate bundles. The quadripartitous stage of *S.* (*S.*) *stubendorffi*, *S.* (*P.*) *middendorffi*, *S.* (*P.*) *pavlovi*, and *S.* (*P.*) *pateraeformis* is, in contrast, characterized by the prevalence of bidichotomous, quasibidichotomous, quadrivirgatitpartitous, and true polyptychous rib bundles in various combinations. The extremes are exemplified by the bidichotomous and the variegated variants of the stage in *S.* (*S.*) *stubendorffi* (see p. 146, 147).

Other morphological features, such as the time of onset of the quadripartitous stage in relation to the beginning of the adult living chamber, the degree of refinement and spacing of its primary and supplementary ribs, the degree of swelling and prominence of its invariably short and bullate primaries, the presence or absence of a decline of ornament from the early to the late phase of the stage, and the degree of a sculptural contrast (or its absence) with the commonly much more refined trivirgatitpartitous sculptural stage, are even more variable. For example, in some representatives of *S. (S.) stubendorffi* the quadripartitous stage occupies the later part of the adult penultimate and the early part of the adult ultimate (i.e. the early part of the adult living chamber) whorl. In the other representatives, however, it is restricted to the early part of the adult ultimate whorl. In yet other representatives, finally, it occupies the bulk of the adult penultimate whorl. Its duration and the character of its termination are unknown in *S.* (*S.*) *stubendorffi* and *S.* (*S.*) n. sp. aff. *stubendorffi* as none of their specimens include the oral half of the adult living chamber. However, it probably extends to its oral end in all representatives of these species (see p. 146, 147). In *S.* (*P.*) *middendorffi* and all other, better known *Pseudoeuryptychites* forms the quadripartitious sculptural stage is markedly displaced backward; it is restricted to parts of the third and second penultimate whorls, persists through one to one and a half of these whorls, and is replaced by the **adult, largely smooth sculptural stage** on the early half of the adult (or last) penultimate whorl (see p. 162, 167). This adult stage is characterized at first by a weakening to a complete loss of the ornament on the flank between the umbilical bullae and the ventral parts of the supplementary ribs and then by a complete or almost complete loss of all ornament, except for the prominent umbilical bullae. This additional adult stage is restricted either to most or all of the adult penultimate and adult ultimate whorls (i.e. in *S.* (*P.*) *middendorffi*) or to the adult ultimate whorl alone (i.e. in the other better known representatives of the subgenus *Pseudoeuryptychites*). See the description of individual *Siberiptychites* forms for further details of the variability of the quadripartitous and adult sculptural stages.

5. The extreme density of primary ribs on the inner whorls of *Siberiptychites*. All known representatives of this genus appear to have at least one and a half as many primaries in those growth stages which are less than 30 mm in diameter than do the most densely ribbed Northwest German *Polyptychites* forms studied by the writers. The *Siberiptychites* forms have between 22 and 30 primaries per whorl in these growth stages in contrast to 15 to 20 primaries on the corresponding inner whorls of the most densely ribbed representatives of *Polyptychites*, such as *P. ascendens*. *P. ramulicosta* (see Pavlow in Pavlow and Lamplugh, 1892, p. 481, Pl. XV, fig. 6a) is exceptional in having 18 to 24 primaries per whorl. However, this species differs from *Siberiptychites* in some other above listed, generically diagnostic features and so is its homoeomorph only.

The following two morphological features may possibly be diagnostic of *Siberiptychites*. However, their taxonomic value remains uncertain and they were provisionally excluded from its diagnosis.

1. As noted by Klimova (1981, p. 80), the earliest sculpture of *Siberiptychites* appears on its venter, in contrast with *Polyptychites* where the earliest sculpture appears at the umbilicus; she states (Jeletzky's translation from Russian):

   > "In the described species (i.e. in *S.* (*S.*) *stubendorffi*; translator's remark), as well as in *Bodylevskites* and *Astieriptychites*, the siphonal ribs are the first to appear. These ribs immediately become strengthened on the siphonal side. The umbilical ribs appear only later."

   The writers cannot comment on the general validity of this potentially important distinction because of an almost complete absence of the corresponding juvenile whorls in their material. However, the earliest sculpture of the only available juvenile specimen of *S.* (*S.*) *stubendorffi* (GSC Cat. 77108; see p. 143 for further details) begins on the umbilical shoulder and extends all the way to the ventral shoulder. Its venter proper is not visible.

2. The presence of feeble to moderate, invariably broad, forward-directed bends of secondary ribs on the venter of intermediate to adult whorls of a number of representatives of the genus. However, this feature may be completely absent in a considerable number of otherwise typical Canadian and Siberian *Siberiptychites* and present in the *Polyptychites ascendens* species group (where it seems to be restricted to larger specimens transitional to *P. brancoi* and to be generally more rarely present and more feebly developed). It only appears as a persistent feature in the descendent, late Valanginian genera *Prodichotomites* and *Dichotomites*.

   The distinctly *Dichotomites*-like forward bends of secondary ribs in the intermediate to adult growth stages of *Siberiptychites* is definitely a homeomorphic phenomenon only, because this genus is restricted to considerably older beds than *Prodichotomites* and *Dichotomites* in the Arctic regions (see p. 133). Furthermore, it does not seem likely that it could indicate any genetic ties between *Siberiptychites* and the late representatives of *Polyptychites* occurring in the uppermost *Polyptychites* beds of Northwest Germany which connect this genus with *Prodichotimites*. This is indicated by the fact that the beds containing *Siberiptychites* in the Sverdrup Basin underlie those containing ammonites typical of the middle to lower *Polyptychites* beds of Northwest Germany, including *P. keyserlingi*. Finally, even stronger *Dichotomites*-like forward bends and inclinations of secondary ribs characterize the genus *Bodylevskites* that occurs at the base of *Siberiptychites*-bearing beds in North- Siberia (Klimova, 1978; Gol'bert et al., 1981, p. 56, 57) and appears to be its immediate ancestor (see p. 20, 21 for further details).

Subgenus *Siberiptychites* Kemper and Jeletzky, 1977

Diagnosis. Medium-sized (terminal adult shell diameter estimated at 120-140 mm) *Siberiptychites* forms in which the characteristic sculpture is weakened but not lost on the preserved early part of the adult last whorl. The generally funnel-like umbilicus is more narrow (20 to 25 per cent) than that of *Polyptychites* and *Pseudoeuryptychites*. The adult external suture line is much more simply and shallowly denticulated than that of *Pseudoeuryptychites* and with only two of its three to four relatively small auxiliary lobes situated on the umbilical wall. The shell ontogeny begins with the first *Euryptychites*-like growth stage and ends, usually, with the sturdy to fairly slender-whorled *Polyptychites*-like growth stage which extends at least onto the early part of the adult last whorl. The umbilical shoulder is widely to narrowly rounded in all known growth stages.

Type-area. Central part of Northern Siberia (Anabar-Khatanga Basin).

Stratigraphy and age. So far as known, the same as for the genus *Siberiptychites* (see p. 133).

Geographical range. Northern Siberia, Arctic Canada (Sverdrup Basin), European Arctic (East Greenland, Spitsbergen).

Discussion. Following the exclusion of *Siberiptychites middendorffi* from the subgenus *Siberiptychites* s. str. (see p. 161-163, 171), this subgenus is restricted to its rootstock consisting of *S*. (*S*.) *stubendorffi* and *S*. (*S*.) n. sp. aff. *stubendorffi* and its relatively slender-whorled development consisting of *S*. (*S*.) *fascicostatus* and *S*. (*S*.) *mira*. Though the stratigraphic relationships of these more slender-whorled forms to the rootstock of the subgenus are poorly understood, they appear to be its younger, somewhat *Prodichotomites*-like offshoot characterized by distinctly discoidal, higher-whorled shells and an increased number of auxiliary lobes. If so, the principal lineage of *Siberiptychites* evolved in a different direction than its *Cadoceras*-like offshoot- the *Pseudoeuryptychites*.

As here restricted, *Siberiptychites* s. str. is characterized by:

1. Its relatively simple adult external suture line which resembles closely its juvenile suture line. All elements of this adult suture line are much more simply and shallowly denticulated than their equivalents in the adult suture of *Pseudoeuryptychites*. Furthermore, it differs in the positioning of the first (and sometimes the second as well; see Figures 53c, 55a) auxiliary lobe on the innermost part of the flank (compare Figures 52b, 52c, 53a-c, 55a-55c with Figures 56a, 56b, 57a-57c). The adult suture of *Siberiptychites* s. str. resembles more closely that of the Northern Siberian representatives of *Bodylevskites* (Klimova, 1978, Figures 5, 6), except in the presence of additional auxiliary lobes and the absence of a pronouncedly retractive (or suspensive) orientation of the umbilical part;
2. The considerably smaller adult shell size, as compared with *Pseudoeuryptychites*. All more nearly completely preserved *Siberiptychites* s. str. forms (i.e. *S*. (*S*.) *stubendorffi* and *S*. (*S*.) n. sp. aff. *stubendorffi*) are estimated to have terminal shell diameters ranging between 120 and 140 mm and the same is belieed to be true of *S*. (*S*.) *fascicostatus* and *S*. (*S*.) *mira*;
3. The retention of a considerable part of the ornament on the early part of the adult last whorl (and presumably on its still unknown oral part also) where a marked weakening of the ribbing is restricted to the mid-flank;
4. The prevalent absence of the second *Euryptychites*-like growth-stage (see p. 136) characteristic of *Pseudoeuryptychites*, including *S*. (*P*.) *middendorffi*. Instead, the intermediate and adult whorls of *Siberiptychites* s. str. have a sturdy (in *S*. (*S*.) *stubendorffi* and *S*. (*S*.) n.sp. aff. *stubendorffi*) to fairly slender (in *S*. (*S*.) *fascicostatus* and *S*. (*S*.) *mira*) *Polyptychites*-like shape and proportions, which persist into the early part of the adult last whorl whenever it is preserved. The sturdy variant of *S*. (*S*.) *stubendorffi* (e.g. Pl. 44, fig. 1A, 1B; Figure 54a) is the only known exception to this rule;
5. The umbilical shoulder of all its representatives being widely to narrowly rounded in all preserved shell growth stages, including the early part of adult last whorl whenever it is preserved;
6. The absence of the initial globular growth stage in the shell ontogeny of *S*. (*S*.) *stubendorffi* where the ontogeny begins with the first *Euryptychites*-like growth stage (see p. 134, 135). Though this more simple shell ontogeny is not yet known in other unsuitably preserved *Siberiptychites* s. str. forms, the appearance of a more complex early shell ontogeny in the most primitive representative of *Pseudoeuryptychites*- *S*. (*P*.) *middendorffi*- suggests its being a constant distinction of the two subgenera (see p. 134, 135 for further details); and
7. The, generally speaking, more narrow (20 to 25 per cent) and deep, commonly almost to quite funnel-like umbilicus. This umbilicus usually (there are exceptions) contrasts with the wider, more shallow, distinctly step-like umbilicus of superficially similar representatives of the genus *Polyptychites* and with the funnel-like but considerably wider (29 to 36 per cent) umbilicus of most *Pseudoeuryptychites* forms. The primitive *S*. (*P*.) *middendorffi* with its *Siberiptychites* s. str.-like umbilicus is an exception. A shallow, step-like umbilicus characterizes, in particular, such homoeomorphs of *S*. (*S*.) *stubendorffi* as *P*. *ramulicosta* (Pavlow, in Pavlow and Lamplugh, Pl. XV, fig. 6a). The characteristically narrower and deeper shape of the umbilicus in *Siberiptychites* s. str. reflects the generally speaking, more involute mode of its coiling in comparison with *Polyptychites*.

The *Polyptychites rectangulatus*-like growth stage is particularly well developed and prolonged, and particularly *Bodylevskites*-like shaped and proportioned, in the ontogeny of *S.* (*S.*) *stubendorffi* (Pavlow, 1914, Pl. V, figs. 6, 7; Klimova, 1981, p. 77, Pl. IX, figs. 1-3; Figure 2; this paper, Pl. 38, figs. 3A, 3B). This feature may possibly be a diagnostic distinction of the entire subgenus *Siberiptychites*. However, the corresponding growth stages are either not exposed or too poorly preserved in all its other representatives to provide any supporting evidence. Therefore, this feature was not included among the diagnostic features of the subgenus.

S. (*S.*) *stubendorffi* is the morphologically most primitive representative of *Siberiptychites* s. str. because of the particularly *Bodylevskites*-like character of the early stages of its shell ontogeny (see p. 135, 136 and earlier in this section). Furthermore, it appears for the first time in the lower subzone of the *Temnoptychites syzranicus* Zone where all other *Siberiptychites* s. str. forms appear to be still absent (see p. 133 for further details). Because of these considerations and some other data provided in the descriptions of the genera *Bodylevskites* and *Siberiptychites* (see p. 20, 21 and below), *S.* (*S.*) *stubendorffi* is considered to be an immediate descendant of *Bodylevskites* (Figure 11). However, no transitional forms connecting these two taxa have been recorded so far.

S. (*S.*) *stubendorffi* is an extremely variable species which includes adult whorl shapes and proportions ranging from relatively slender, *Polyptychites-beani*-like (and also somewhat *Bodylevskites*-like) variant (Klimova, 1981, Pl. IX, figs. 4, 4a; this paper, Pl. 36, fig. 1; Figure 54b), through the *Polyptychites keyserlingi*-like variant (Pl. 37, fig. 2B, 2C; Pl. 54, fig. 1A, 1B) to the essentially (i.e. except for the narrowly rounded umbilical shoulder) *Euryptychites*-like variant (Pl. 44, figs. 1A, 1B; Figure 54a). Therefore, and because of the presence of morphologically intermediate forms, it is easy to derive all other *Siberiptychites* s. str. forms and the subgenus *Pseudoeuryptychites* directly from *S.* (*S.*) *stubendorffi*. The slightly younger *S.* (*S.*) n. sp. aff. *stubendorffi* is morphologically similar to and appears to intergrade with the slender variant of *S.* (*S.*) *stubendorffi*. Therefore, it is considered to be its but slightly modified, immediate descendant. The same appears to be true of *S.* (*S.*) *fascicostatus* (and probably also of the Northern Siberian *S.* (*S.*) *mira*) which closely resembles *S.* (*S.*) n. sp. aff. *stubendorffi* and the slender variant of *S.* (*S.*) *stubendorffi* in most of its diagnostic morphological features. The more slender whorl shape, the presence of the fourth auxiliary lobe already in the intermediate suture line, and the positioning of the second auxiliary lobe on the flank of *S.* (*S.*) *fascicostatus* do not appear to taxonomically significant on the supraspecific level. Finally, *S.* (*P.*) *middendorffi* is so similar morphologically to the intermediate and sturdy variants of *S.* (*S.*) *stubendorffi* in such important features as the general shell shape and proportions, the character of the early and late juvenile external suture line, and the broadly to narrowly rounded appearance of the umbilical shoulder, that it can be derived directly from one of these variants. However, *S.* (*P.*) *middendorffi* is already *Pseudoeuryptychites*-like in a number of other, even more important morphological features (see p. 161-163, 171 for further details) and is morphologically closer to the latter subgenus in which it is placed.

Siberiptychites (*Siberiptychites*) *stubendorffi*
(Schmidt, 1872)

Pl. 32, fig. 3; Pl. 34, fig. 2; Pl. 36, fig. 1; Pl. 37, fig. 2; Pl. 38, fig. 3; Pl. 39, fig. 1; Pl. 42, fig. 4; Pl. 43, fig. 3; Pl. 44, figs. 1, 3; Figures 52, 53, 54a, 54b.

Synonymy

1872	*Ammonites polyptychus* var. *Stubendorffi* Schmidt, p. 133, Pl. III, figs. 14a, 14b; Pl. IIIa, fig. 3; non Pl. III, fig. 13a, 13b.
1914	*Polyptychites stubendorffi* Pavlow, p. 29, Pl. V, figs. 5, 6, 7; Pl. VI, fig. 1.
1914	*Polyptychites* sp. cf. *ramulicosta* Pavlow, p. 24, Pl. V, figs. 1a, 1b.
?1929	*Polyptychites* cf. *ramulicosta* Frebold, p. 9, 10; Pl. IV, figs. 1a, 1b.
1949	*Polyptychites stubendorffi* Bodylevsky in Berg et al., p. 204, Pl. LVI, fig. 1 (non Pl. LVI, fig. 2); Text-fig. 28.
1953	*Polyptychites stubendorffi* Krimgolts in Krimgolts, Petrova and Pchelintsev, p. 79-82, Pl. XI, fig. 3, Text-fig. 14.
1953	*Polyptychites* cf. *middendorffi* Donovan, p. 102, 103; Pl. 21, figs. 2, 2b.
1964	*Polyptychites stubendorffi* var. *middendorffi* Jeletzky, p. 46, 48; Pl. IX, fig. 1; Pl. X, fig. 3, non Pl. X, fig. 5.
1977	*Polyptychites* (*Siberiptychites*) *densicosta* Kemper, p. 3.
1977	*Polyptychites* (*Siberiptychites*) *stubendorffi* Kemper, p. 3, etc. (in part).
1980	*Polyptychites* aff. *ramulicosta* Yershova, p. 79, Pl. VI, fig. 2.
1981	*Siberiptychites stubendorffi* Klimova, p. 74, Pl. IX, figs. 1-6; Figs. 1-3.

Type specimen. Klimova (1981, p. 75) has formally designated the cotype of *Ammonites polyptychus* Keyserling var. *stubendorffi* reproduced by Schmidt (1872) in Pl. III, fig. 13 as the lectotype of *Siberiptychites stubendorffi* (Schmidt, 1872). However, this selection is inadmissible as that particular specimen was removed from the species by Pavlow (1914, p. 29, 30, 34-36, Pls. VIII-X) and described as *Polyptychites tschekanovskii* n. sp. It is the holotype of that species by monotypy. Only the remaining two cotypes of *A. polyptychus* var. *stubendorffi* reproduced in Pl. III, fig. 14 and Pl. IIIa, fig. 3 of Schmidt's (1872) paper are now available for selection as lectotype. These specimens were redescribed and excellently refigured by Pavlow (1914, p. 29-31, Pl. V, fig. 6; Pl. VI, fig. 1). Designation of a late juvenile specimen being obviously inadvisable, the writers propose herewith to select the larger, presumably adult cotype of Schmidt (1872, Pl. III, fig. 14) as the lectotype of *Siberiptychites* *stubendorffi*. The description and figure of Schmidt (l. cit.) being insufficient for an exact interpretation of the original specimen, one has to depend on its description and excellent illustrations by Pavlow (1914, p. 29-31, Pl. VI, figs. 1a-1c).

Material. Nine almost complete to fragmentary but readily determinable specimens from the Sverdrup Basin (GSC loc. 37867, 91310, 91311, 91354 and 93760).

Diagnosis. A medium-sized (shell diameter of almost complete adults not known to exceed 120 mm) *Siberiptychites*, the advanced to adult representatives of which are moderately to rather low whorled (whorl height fluctuates between 88 and 60 per cent of its width). Adult external suture line is characterized by simple and shallow denticulation and the positioning of the first auxiliary lobe on the adumbilical part of the flank. The *Bodylevskites*-like shape and cross-section of later juvenile whorls are exceptionally well expressed and the first *Euryptychites*-like growth stage extends to the protoconch replacing the globular growth stage. The predominantly quadripartitous ornament of adult penultimate whorl either retains its strength or is weakened but not obliterated on the early part of adult living chamber.

Measurements (in mm)

Specimen	Shell diameter	Umbilicus	Whorl's height wh 1	wh 2	Whorl's thickness wth 1	wth 2	Ratio of height/ width of the whorl
GSC Cat. 77115 (sturdy variant)	93 mm (estim.)	19.5 (21%) (estim.)	37 (40%)	– (39%)	57 (?)	—	60%
GSC Cat. 77116 (interm. variant)	84	20 (24%)	36 (43%)	28 (33%)	45	35	80%
GSC Cat. 77101 (slender variant)	71	17 (24%)	30 (42%)	23 (34%)	36	29	88%

Description

General remarks. Until recently the available material of *S*. (*S*.) *stubendorffi* was scarce, stratigraphically uncertain and represented exclusively (Donovan, 1953; Krimgolts et al., 1953) or almost exclusively (Schmidt, 1872; Pavlow, 1914) by advanced to adult but entirely septate shells. This precluded a detailed study of its time range and ontogenetic development. Klimova (1978, 1981) was apparently the first to fill in the gap in our knowledge of the ontogenetic development of *S*. (*S*.) *stubendorffi*. Her studies confirmed the correctness of Schmidt's (1872, Pl. IIIa, fig. 3) and Pavlow's (1914, p. 29, Pl. V, figs. 6, 7) assignment of slender, *Bodylevskites*-like early to mid-juvenile shells to *S*. (*S*.) *stubendorffi*.

This study uses 9 partly stratigraphically collected Canadian specimens of advanced to adult *S*. (*S*.) *stubendorffi*. Some shells retain early parts of presumably intermediate to adult living chambers. This material includes only one juvenile and no halfgrown representatives of the species and so does not add anything to the previously discussed (p. 136-138) results of Klimova's (1981) study of these growth stages of *S*. (*S*.) *stubendorffi*. Furthermore, an attempt is made to re-evaluate all previously described and figured Eurasian representatives of the species in order to elucidate the range of its infraspecific variability and its stratigraphic range.

The Canadian material includes 5 specimens from bed 16, of Kemper (1977) which include typical, morphologically average representatives of *S*. (*S*.) *stubendorffi* (e.g. GSC Cat. 77116; Pl. 44, fig. 3), its considerably sturdier representatives (e.g. GSC Cat. 77115; Pl. 44, fig. 1) that match closely the lectotype (Pavlow, 1914, Pl. VI, fig. 1), and the considerably more slender *Polyptychites beani*-like representatives (e.g. GSC Cat. No. 77101; Pl. 36, fig. 1). This range of variation in the material collected from the same concretionary bed has decisively influenced the writers' interpretation of *S*. (*S*.) *stubendorffi*. It prompted them to exclude the *S*. (*S*.) *stubendorffi*-like shells occurring in the overlying bed 14 of the same section, which were previously included in this species (Kemper, 1977, p. 3, Figure 3).

Whorl shape and proportions. The only late juvenile Canadian shell (Pl. 38, fig. 3A, 3B) has the terminal diameter of about 13 mm. This somewhat distorted, slender and discoidal whorl is similar to the equivalent whorls of the North Siberian *S*. (*S*.) *stubendorffi* described and figured by Klimova (1981, p. 75, 76; Pl. IX, figs. 1, 1a, 1b, 2a, 2b; Figure 2). Earlier and later (up to 40 mm) juvenile and intermediate whorls are unavailable. However, they are assumed to be similar to the equivalent whorls of the North Siberian *S*. (*S*.) *stubendorffi* described and figured by Schmidt (1872, Pl. IIIa, fig. 1), Pavlow (1914, p. 29, 30; Pl. V, figs. 6, 7), and Klimova (1981, p. 75-77; Pl. IX, figs. 3a, 3b, 4, 4a, 5; Figure 2).

All subsequent growth stages, that range from the shell diameter of about 50 mm (e.g. Pl. 34, fig. 2) to that of about 100 mm (e.g. Pl. 38, fig. 3; Pl. 39, fig. 1) vary strongly in their shape and proportions (see Table of Measurements and fossil plates for further details). The following three morphological variants were distinguished:

1. Sturdy variant with rather *Euryptychites*-like shape and proportions. Its whorl has approximately regularly rounded flanks and venter which results in a complete (e.g. Pl. 44, fig. 1B) to almost complete (Pl. 39, fig. 1C) absence of a ventral shoulder. The excellently defined umbilical shoulder is narrowly rounded in contrast to the subgenus *Pseudoeuryptychites*. This whorl is always considerably wider than high (i.e. from 60 to 70 per cent). The greatest width is always situated at the umbilical shoulder. The umbilical wall is straight to but slightly convex and forms angles of 50 to 60 degrees with the plane of symmetry. Succeeding whorls cover 85 to 95 per cent of the preceeding whorls. In combination with the orientation of the umbilical wall, this results in a funnel-like shape of a deep but only moderately involute (20-24 per cent) umbilicus. This variant, the advanced and adult whorls of which mimic the inter-

mediate whorls of S. (*Pseudoeuryptychites*) *middendorfi*, is typified by the specimens GSC Cat. 17244 (Pl. 39, fig. 1) and 77115 (Pl. 44, fig. 1). It also includes the North Siberian lectotype and the specimen figured by Krimgolts et al. (1953, Pl. XI, fig. 3). In the largest Canadian examples (e.g. Pl. 39, fig. 1) the living chamber begins at the shell diameter of about 90 mm but the lectotype is fully septate to its oral end at the diameter of about 100 mm (Pavlow, 1914, Pl. VI, figs. 1a, 1b). This living chamber is inferred to be adult for reasons presented below (see p. 146) and the sturdy variant appears to have about the same adult size as the intermediate variant where the presumably adult living chamber mostly, but not always (see below for further details), begins at a comparable size.

2. Morphologically intermediate variant with moderately sturdy (i.e. *Polyptychites keyserlingi*-like) and rounded-rectangular advanced to adult whorls. The distinctly flattened venter is separated from the flanks by a very broadly rounded but distinct ventral shoulder. The whorls are only moderately wider than high (e.g. from 75 to 82 per cent). The shape and proportions of the umbilical shoulder, umbilical wall, and the umbilicus are similar to those of the sturdy variant. The variant is typified by specimens reproduced in Pl. 32, fig. 3, Pl. 44, fig. 3, Pl. 54, fig. 1, and the North Siberian specimen figured by Pavlow (1914, Pl. V, fig. 5). Specimen reproduced in Pl. 38, fig. 3, the umbilicus of which exposes the only known Canadian juvenile whorl, and the unfigured specimen GSC Cat. 93760/1 are morphologically transitional to the sturdy variant; and
3. The slender or *Polyptychites beani*-like variant with a halfoval to obtusely eggshaped, either regularly but narrowly arched cross-section (e.g. Klimova, 1981, Pl. IX, fig. 4a) or narrowly arched, nearly flatflanked and flatventered whorl (e.g. Pl. 36, fig. 1C). The latter has, accordingly, a distinctly trapezoidal, adventrally contracting cross-section, which is somewhat transitional to that of the next younger *Siberiptychites* (*Siberiptychites*) n. sp. aff. *stubendorffi* (Pl. 38, fig. 1B; Pl. 42, fig. 1; Pl. 63, fig. 2C; Figures 54a-54c). The whorl cross-section is not much wider than high (e.g. from 80 to 88 per cent: compare Pl. 36, fig. 1C and Pl. 44, fig. 2B). The shape and proportions of the umbilical shoulder, umbilical wall, and the umbilicus resemble closely those of the other two variants, except that the umbilicus is more shallow (e.g. Pl. 36, figs. 1A, 1D) than that of the sturdy variant. The slender variant is represented by the Canadian specimens GSC Cat. 77101 and 77111 and the North Siberian specimen figured by Klimova (1981, Pl. IX, figs. 1-6, Figures 1-3).

Sculpture. In addition to the uniquely complex ontogenetic development of the sculpture characteristic of all *Siberiptychites* species (see p. 136-139), the sculpture of S. (S.) *stubendorffi* varies pronouncedly in most of the individual sculptural stages. This section attempts to describe the resulting, complex variation patterns, because of which no two specimens of our species are exactly alike.

The sculpture of juvenile and intermediate whorls is known only in the specimen GSC Cat. 77108 (Pl. 38, figs. 3A, 3B). The early two-thirds of this whorl, that begins at the estimated shell diameter of 7.5 mm, exhibits the end part of the smooth sculptural stage which lacks any ribbing on the flanks and the umbilical wall (the venter is not exposed). Only occasional, barely perceptible striae and several relatively feeble, forward inclined, and flexuous constrictions are visible on this segment which should represent some part of the fourth whorl from the protoconch according to Klimova's (1981, p. 77, 78, Pl. IX, figs. 1-3) results. The oral one-third, beginning with the shell diameter of about 11 mm, exposes the very beginning of the *Bodylevskites*-like sculptural stage. The few earliest primary ribs visible there begin either on the illdefined umbilical shoulder or on the umbilical wall proper. These fairly prominent, roundtopped ribs either persist singly all across the flank and the ventral shoulder (the venter is not exposed) or split into two equally prominent and roundtopped secondaries within the lower third of the flank. All ribs are forward inclined and somewhat flexuous throughout. They either retain their strength throughout or become distinctly strengthened adventrally. The main, more typical part of this sculptural stage is not reached at the oral end of the whorl. However, it is assumed to be essentially similar to that described by Klimova (1981, p. 77, 78; Pl. IX, figs. 1-3). Only the lower parts of primary ribs of the main *Bodylevskites*-like sculptural stage were actually observed in the Canadian material; they are fine, strongly elevated and pinched throughout and count from 26 to 30 per whorl.

The predominantly dichotomous stage is only well exposed in the specimen GSC Cat. 77111 (Pl. 42, fig. 4; Pl. 43, fig. 3; Pl. 44, fig. 2A, 2B and Pl. 64, fig. 2). The earliest one-half whorl (Pl. 44, fig. 2A; Pl. 64, fig. 2), confined between the shell diameters of about 38 and 45 mm, is ornamented by ten simple dichotomous rib bundles intercalated with two trivirgatitpartitous and one trifasciculate rib bundles. It also exposes two well developed, forward inclined constrictions adorally flanked by a single rib each. The beginning of this sculptural stage is not exposed. The about 15 primaries (estimated 30 per whorl) occurring on this half-whorl begin as faint and thin ridges on the outer half of markedly convex umbilical wall, leaving its inner half smooth. They strengthen gradually across the regularly rounded umbilical shoulder and across either the lowermost part or the lower one-third to one-half of the flank to their branching point. None become either bullate or even slightly thickened anywhere. The internal moulds of primaries are roundtopped and low but they are sharptopped and fairly high whenever shell-covered. The primaries are very closely spaced, with the somewhat forward concave interspaces being either equal to or slightly wider than their width. The primaries are strongly to markedly adorally inclined throughout their length and approximately straight, except on the umbilical shoulder where they are feebly forward concave. This contrasts with their comma-like shape in the later structural stages.

The supplementary ribs are either as thick as the primaries near their branching point or but slightly finer than they. They are slightly (the posterior ribs) to distinctly (the anterior ribs) forward inclined and mostly straight throughout the flank. Only a few supplementaries are slightly flexuous (forward convex). They form slight forward convex bends on the venter where they are not in the least weakened (Pl. 44, fig. 2B). There are 35 or 36 supplementaries per half whorl, which projects to some 70 supplementaries per whorl.

A similar but less well preserved example of the simple dichotomous stage is provided by an about one-sixth of the whorl long segment of GSC Cat. 93760/1 (unfigured) at the shell diameter of about 45 mm. Another example of this sculptural stage is present in the specimen GSC Cat. 77104 (Pl. 37, fig. 2A) where a short segment of its earlier whorl (estimated shell diameter of 45 to 50 mm) is exposed by a break in the last preserved whorl.

The earliest part of the whorl figured by Donovan (1953, p. 102, 103; Pl. 21, fig. 2) as "*Polyptychites* cf. *middendorffi*" apparently exposes the end part of the predominantly dichotomous sculptural stage. It appears to be ornamented by ten to (?) twelve simple dichotomous bundles and seems to lack any other types of bundles. The predominantly dichotomous sculptural stage is not definitively recognizable in any previously figured North Siberian example of *S.* (*S.*) *stubendorffi*.

The duration of the predominantly dichotomous stage cannot be conclusively determined from its presently known partial examples. It probably extends over one to one and a half whorl and follows immediately the *Bodylevskites*-like sculptural stage.

The predominantly trivirgatitpartitious sculptural stage is much more common (e.g. Pl. 32, fig. 3; Pl. 34, fig. 2A; Pl. 36, fig. 1A; Pl. 37, figs. 2A, 2B; Pl. 38, fig. 3A; Pl. 42, fig. 3; Pl. 44, figs. 1A, 3) than the preceding predominantly dichotomous stage.

One morphological extreme is the **densely ribbed variant** of the stage characterized by a relatively greater refinement and density of supplementary ribs which either remain more or less uniform throughout the stage or increase only slightly in its terminal part. These distinctions are combined with a relatively minor increase of the sparcity and thickening of primaries and secondaries in the succeeding predominantly quadripartitous stage.

This variant is best exemplified by the sturdy specimen GSC Cat. 77115 (Pl. 44, figs. 1A, 1B) where it begins at the earliest visible part of the whorl with the shell diameter of about 65 mm and extends over at least its early two-thirds to the shell diameter of about 84 mm. The beginning of the trivirgatitpartitous stage is not exposed and its termination is largely obscured by a deep weathering of the remaining oral part of the whorl (Pl. 44, fig. 1A) which ends at the shell diameter of about 94 mm. The whorl bears 26 primary and 90 to 91 supplementary ribs. The distinctly backward inclined primaries apparently begin within the outer half of the umbilical wall. They form distinct, forward-convex, comma-like bends on the umbilical shoulder and the lowermost flank until they become slightly inclined forward closely below the branching point which is invariably situated within the lower part of the flank and commonly lies within its lowermost quarter.

When shell-covered, the primaries and the secondaries alike are attenuated, sharptopped, and relatively markedly elevated. However, their internal casts are relatively lower, relatively thickened, and roundtopped. The primaries are from only slightly to about two times thicker than the supplementaries in either type of preservation. They are nonbullate, being neither distinctly elevated nor appreciably swollen on the umbilical shoulder.

The concave roundbottomed interspaces between the primaries are either about as wide as their relatively widened internal casts or up to one and a half times wider than the latter. The primaries do not become either any sparcer or distinctly heavier built adorally to the whorl's end. The supplementary ribs are even more crowded than the primaries, the width of their interspaces being either equal to or only slightly wider than their relatively widened internal casts. All supplementaries are approximately straight but distinctly forward inclined throughout the flank. They are not weakened on the venter where they are distinctly but very broadly arched forward (Pl. 44, fig. 1B). Regardless of their type of preservation, the supplementary ribs gradually become more crowded, relatively lower and relatively more roundtopped adorally all the way to the whorl's end. However, these changes are much less than in the sparcely ribbed variant of trivirgatitpartitous stage.

The end part of the densely ribbed variant is typically developed on the early part of the only exposed, last whorl of GSC Cat. 77116 (Pl. 44, fig. 3; Pl. 54, fig. 1). The largely shell-covered primary ribs of this end part of the stage are probably more advanced than the oralmost primaries of GSC Cat. 77115. They are comma-like forward bent, distinctly elevated, roundtopped (where poorly preserved) to fairly sharptopped (where best preserved), distinctly thickened bulges. The concave interspaces between these bullae are about as wide as they are on the earliest part of the whorl but begin to widen markedly at about the end of the phragmocone where the trivirgatitpartitous stage ends. On the left flank a large pathological mound greatly disturbs the ribbing habit just at that point. The whole whorl has 21 primaries and between 90 and 95 supplementaries.

The septate early half of the last preserved, apparently adult penultimate to adult ultimate whorl of GSC Cat. 77096 (Pl. 32, fig. 3) exhibits yet another example of the late part of the densely ribbed variant of the trivirgatitpartitous stage. This example is similar to that of the specimen GSC Cat. 77116 in the degree of refinement, density, and orientation of its primary and secondary ribs. However, its primaries are nonbullate (as in GSC Cat. 77115) and it displays an appreciably lesser contrast between the density of its trivirgatitous supplementaries and that of the supplementaries of the succeeding quadripartitous sculptural stage.

The East Greenland "*Polyptychites* cf. *middendorffi*" of Donovan (1953, p. 102, 103; Pl. 21, fig. 2) also exhibits the densely ribbed variant of the trivirgatitpartitous stage on the oral three-quarters of its last whorl. This example is similar morphologically to that displayed by the specimen GSC Cat. 77115. None of the previously figured North Siberian representatives of *S.* (*S.*) *stubendorffi* is known to exhibit this particular variant of the trivirgatitpartitous sculptural phase.

The densely ribbed variant of the trivirgatitpartitous stage follows immediately the predominantly dichotomous stage and is followed immediately by the quadripartitous stage. Its complete extent remains uncertain but it is inferred to last between one and one and a half whorls and to be confined either to the second and/or the last adult penultimate whorl before the beginning of the adult living chamber.

The other morphological extreme is the **sparcely ribbed variant** of trivirgatitpartitous stage characterized by a greater sparcity of supplementary ribs as compared with the densely ribbed variant. In this variant the particularly sparce, attenuated and sharptopped supplementaries of its early part become much more delicate, low, and crowded in its late part (e.g. GSC Cat. 77104; Pl. 37, fig. 2A, 2B or GSC Cat. 17244; Pl. 39, fig. 1A-1C). This results in a greater morphological contrast between these two parts of the sparcely ribbed variant as compared with those of the densely ribbed variant. Furthermore, the variant exhibits a pronounced morphological contrast between the very strongly refined and crowded habit of its late part and the much coarser and sparcer habit of the succeeding predominantly quadrivirgatitpartitous stage.

This variant is best exemplified by the last preserved whorl of the specimen GSC Cat. 77104 (Pl. 37, fig. 2A, 2B) which is ornamented by typical trivirgatitpartitous bundles, except for the oralmost quarter where the predominantly quadrivirgatitpartitous sculptural stage begins. The whorl bears 23 primary ribs and only (typically for the variant) 81 or 82 supplementary ribs. The trivirgatitpartitous stage appears to begin within the oralmost quarter of the preceding whorl and to extend for slightly less than one whorl as a short exposed segment of the earlier part of that whorl displays a few simple dichotomous bundles. The primary ribs begin either on the outer half of the umbilical wall or on the inner surface of the umbilical shoulder where they are inclined backward at 60 to 70 degrees. They form forward concave, comma-like bends on this shoulder and become distinctly forward concave and forward inclined on its outer surface. This orientation is maintained to their branching point that is situated on the lower third to the lower one-quarter of the flank, becoming, as a rule, lowered oralward. These primaries are distinctly shorter than those of other examples of the sparcely ribbed variant of the stage and about as long as those of its densely ribbed variant. The posterior secondary bifurcates again at or somewhat above the midflank (Pl. 37, fig. 2A). The resulting, approximately straight supplementary ribs are all inclined forward. They are definitely not weakened and may be strengthened on the venter where they broadly and gently arch forward.

Regardless of their preservation, the primary and supplementary ribs of the early half of the whorl are considerably more sparce, prominent, and slender than those of any other example of either the sparcely ribbed or the closely ribbed variant of trivirgatitpartitous stage. Their internal casts are at least as high as wide (i.e. at the base), upward attenuated, and narrowly rounded (Pl. 37, fig. 2A, 2B). The shell-covered, well preserved ribs are two to three times higher than wide (i.e. at the base) and sharptopped. On the early part of the whorl the roundbottomed interspaces between the primaries are two to three times wider than the latter while the interspaces between the supplementaries are only twice as wide, except between their bundles. On the oral half of the whorl the primaries become increasingly swollen and elevated on the umbilical shoulder and become slender, weltlike bullae near the phragmocone's end. Their internal casts are low and roundtopped but their shell-covered examples are much more elevated and fairly sharptopped. The width of the interspaces between the bullae are reduced in relation to the interspaces on the early part of the whorl and the same is true of the interspaces between their supplementaries which are about halved. Concurrently, the supplementaries become much less prominent (wider than high), relatively more attenuated, and broadly roundtopped in the internal cast and shell covered preservation alike. This results in a strongly contrasting appearance of the supplementary ribs on the early and late parts of the whorl that is characteristic of the sparcely ribbed variant of the trivirgatitpartitous stage. A gradual attenuation, a pronounced increase of the density of supplementary ribs, and an equally pronounced decrease of their height and acuteness toward the end of the sparcely ribbed variant of the trivirgatitpartitous stage is even stronger expressed in the specimen GSC Cat. 17224 (Pl. 39, fig. 1A-1C). In this specimen, as in the specimen GSC Cat. 77104, this trend is abruptly reversed at the end of the trivirgatitpartitous stage.

Among foreign specimens, that figured by Pavlow (1914, Pl. V, fig. 5a, 5b) exhibits the same development of the late part of the trivirgatitpartitous stage as does the Canadian specimen GSC Cat. 77104.

In the third and last variant of the trivirgatitpartitous stage relatively sparce, sharptopped and prominent supplementary ribs persist throughout its extent resulting in a strong lessening to an almost complete absence of contrast between its early and late phases. This **subevenly spaced variant** is typified by the GSC Cat. 77101 (Pl. 36, figs. 1A-1C) in which the last preserved, only exposed whorl with the shell diameters ranging from about 50 to about 71 mm is entirely occupied by the trivirgatitpartitous stage. Neither the beginning nor the end of this presumably almost entirely exposed (i.e. judging by its other examples) stage is visible. There are 22 primaries and 71 or 72 supplementaries on this whorl where the prevalent trivirgatitpartitous bundles alternate with one *ramulicosta*-like quadrivirgatitpartitous bundle and two quasifasciculate bundles. On its early half the primaries and secondaries are similar to those of the sparcely ribbed variant of the GSC Cat. 77104 (Pl. 37, fig. 2A, 2B), except for being almost subtransversal on the venter. Their spacing, height, and sharpness decrease gradually adorally but they do not become either as crowded or as refined and low on the oral half of the whorl as do the ribs of the sparcely ribbed variant.

The other example of the subevenly spaced variant (GSC Cat. 77111; Pl. 42, fig. 4; Pl. 43, fig. 3) displays only its early part on the oral half of the last whorl which merges into the simple dichotomous ornament on its early half. The primaries of GSC Cat. 77111 are considerably more attenuated and less elevated than those of GSC Cat. 77101. Furthermore, they are narrowly roundtopped, only slightly convex across the umbilical shoulder, and only begin to thicken slightly at the whorl's oral end (shell diameter of about 62 mm). The essentially similar supplementaries are also relatively more refined and considerably lower. However, all ribs of GSC Cat. 77111 are about as widely spaced and sparce as those of GSC Cat. 77101. There are 26 primaries and about 75 secondaries on the last whorl of GSC Cat. 77111. The early and late parts of its trivirgatitpartitous stage do not contrast as the supplementaries are only slightly more crowded and refined near the oral end of the whorl.

The North Siberian "*Polyptychites* sp. cf. *ramulicosta*" (Pavlow, 1914, Pl. V, fig. 1a, 1b) is the only foreign example of the subequally spaced variant. Its late part exposed on the early part of the last whorl has even sparser and heavier built supplementaries than that of the specimen GSC Cat. 77101.

The last known sculptural stage is the **predominantly quadripartitous stage** which replaces the trivirgatitpartitous stage either near the beginning of the adult penultimate whorl (e.g. GSC Cat. 77108; Pl. 38, fig. 3A) or on the later part of this whorl (e.g. GSC Cat. 77104; Pl. 37, fig. 2B) or, finally, in the proximity of the adult living chamber (e.g. GSC Cat. 17244; Pl. 39, fig. 1A, 1B). It extends over one to two whorls but its full extent is not known as the oral half of adult living chamber is not preserved in any of the studied specimens. The predominantly quadripartitous stage is the adult growth stage of *S.* (*S.*) *stubendorffi* because:

1. A number of its Canadian and foreign examples extend onto the early part of the living chamber (e.g. GSC Cat. 17244, 77104, 77096, 77116; Pavlow, 1914, Pl. V, fig. 1; Klimova, 1981, Pl. IX, fig. 6);
2. The terminal external sutures of some of these examples are distinctly approximated and simplified (e.g. GSC Cat. 77104 and 77116; Pl. 37, fig. 2; Pl. 44, fig. 3; Figures 52b, 52c); and
3. The quadripartitous sculpture commonly, though not always, weakens considerably and may be almost obliterated on the flanks of the last whorl that either immediately preceds or includes the living chamber.

Because of the above relationships, *S.* (*S.*) *stubendorffi* appears to be a medium-sized representative of the subgenus *Siberiptychites* the terminal shell diameter of which does not, as a rule, exceed 120 to 130 mm.

The Canadian and Eurasian examples of the quadripartitous stage are classified infraspecifically on the ratio of bidichotomous rib bundles to their other types (e.g. quadrvirgatitpartitous, quadrifasciculate, trivirgatitpartitous, etc.). One morphological extreme is the **bidichotomous variant** with sparce to very sparce and more or less distant ribs arranged exclusively to almost exclusively into bidichotomous bundles. This variant, which is restricted essentially to the adult living chamber, is typified by the specimen GSC Cat. 17224 (Pl. 39, Fig. 1A, 1B) in which the exclusively bidichotomous bundles are restricted to the oral three-fifths (largely represented by the adult living chamber) of the last whorl. One deep and wide constriction occurs near its broken off oral end. The primaries and supplementaries are considerably coarser and much more widely spaced (interspaces are three times wider than the ribs) than those of the adjacent late part of the trivirgatitpartitous stage. They project to only 15-16 primaries and 57-60 supplementaries per whorl. Very short primaries are essentially restricted to the umbilical shoulder, only slightly bullate, and forward convex. The posterior supplementaries of each bundle are subradially oriented while their anterior supplementaries are forward inclined; they are all approximately straight, and only slightly arched forward on the venter. The ribs are distinctly strengthened on the venter as compared with the flanks.

The specimen GSC Cat. 77116 (Pl. 44, fig. 3; Pl. 54, fig. 1) is another good example of the bidichotomous variant. The oral half of this whorl (again the early part of adult living chamber) is ornamented predominantly by the bidichotomous and quasibidichotomous rib bundles intercalated with two tridichotomous and one trivirgatitpartitous bundles. Their primaries and supplementaries are distinctly coarser and sparser than those of the preceding densely ribbed example of the trivirgatitpartitous stage. The short, comma-like bent primaries are markedly bullate but closely spaced before the end of the trivirgatitpartitous stage. However, they become considerably more widely spaced at the onset of the quadripartitous stage. Generally speaking, the contrast between the late trivirgatitpartitous and the quadripartitous structural stages is much less in GSC Cat. 77116 than in the specimen GSC Cat. 17224. Therefore, this example of the stage is somewhat transitional morphologically to its variegated variant described below. Unlike the specimen GSC Cat. 17224, the sculpture of the quadripartitous stage of the specimen GSC Cat. 77116 becomes distinctly weakened to almost obliterated on the flanks near its oral end (Pl. 54, fig. 1A). The ribs of GSC No. 77116 project to only 16-17 primaries and 50-55 supplementaries per adult ultimate whorl.

Of the foreign examples of *S.* (*S.*) *stubendorffi* only "*Polyptychites* sp. cf. *ramulicosta*" of Pavlow (1914, Pl. V, fig. 1) appears to exhibit the bidichotomous variant of the quadripartitous stage on the oral one half to ?two-thirds of its last whorl. This example resembles closely that of the GSC Cat. 77116 but there is even less coarsening and sparsening of its primaries and supplementaries as compared with those of its late trivirgatitpartitous stage and the sculpture of the former does not weaken appreciably near the oral end of the whorl.

The other morphological extreme of the quadripartitous stage is the **variegated variant** characterized by an association of several quadripartitous types of bundles, among which the bidichotomous type is subordinate to rare, and a complete to almost complete absence of coarsening and sparsening of the primary and supplementary ribs throughout its known extent. This variant begins either near (possibly even earlier) the beginning of adult penultimate whorl or somewhere within its early half and extends onto the early part of the ultimate whorl.

The variegated variant is typified by the last whorl of the specimen GSC Cat. 77108 (Pl. 38, fig. 3A) which is septate right to its oral end at the shell diameter of about 100 mm. Its oral seven-eighths occupied by the variegated variant exhibits a somewhat irregular alternation of quadrivirgatitpartitous (prevalent), trivirgatitpartitous (relatively rare), quadrifasciculate (rare), regularly to irregularly bidichotomous (rare), and true polyptychous (rare) rib bundles. This sculpture is so weakened on the flanks of the oralmost third of the whorl that it is difficult to discern the bundling habit. The short, forward concave, and distinctly swollen (bullate) primary ribs extend from the outer umbilical wall to the lowermost flank where they bifurcate. These bullae are sharp-topped when shell-covered but their internal moulds are roundtopped and distinctly widened. Their interspaces are about two times wider than they. The supplementary ribs gradually decrease in height, prominence, and density adorally within the quadripartitous stage so that there is hardly any morphological contrast with the preceding final part of the trivirgatitpartitous stage. All supplementaries begin on the lower half of the flank (Pl. 38, fig. 3A). The posterior supplementaries of all bundles are subradial to slightly forward inclined while the anterior ones are stronger inclined. The inclination of all supplementaries increases toward the venter where they form slight and broad, forward convex loops and are just as prominent as on the flanks (except in the oralmost third of the whorl). Two well defined constrictions occur on the oral half of the whorl.

The specimen GSC Cat. 77096 (Pl. 32, fig. 3) provides an example of the variegated variant that resembles closely that of the GSC Cat. 77108, except in including about one-third (5 out of 16) of bidichotomous bundles. Furthermore, its primaries and supplementaries become gradually more sparse (and also more prominent, except on the flanks where they progressively weaken on the oral half of the whorl) oralward until their interspaces become 1 1/2 to 2 times wider than they. The entire whorl bears 21 or 22 primaries and 92 to 95 supplementaries.

The quadripartitous stage that occupies the oralmost one-quarter whorl of the specimen GSC Cat. 77104 (Pl. 37, fig. 2B) is morphologically transitional between its bidichotomous and variegated variants in the ratio of bidichotomous to other bundles, the degree of density and refinement of the supplementaries, and in the spacing of slightly bullate primaries.

The quadripartitous stage of the lectotype of the species (Pavlow, 1914, Pl. VI, fig. 1) is typical of its variegated variant. It occupies all of its last, entirely septate (presumably adult penultimate) whorl with the terminal diameter of about 110 mm. Its early one-third is ornamented by well formed, predominantly quadripartitous bundles, including bidichotomous (common), trivirgatitpartitous (fairly rare), true polyptychous, and ?trifasciculate bundles, and one prominent constriction. The sculpture becomes markedly weakened and then almost obliterated on the flanks of the oral two-thirds of the whorl while the originally bullate primaries are transformed into prominent nodes. Other examples of the variegated variant of this stage are provided by the oral two-thirds of the North Siberian whorl figured by Pavlow (1914, Pl. V, fig. 5) and the oralmost two whorls of the specimen figured by Klimova (1981, p. 78, Pl. IX, figs. 4a, 4b).

The bidichotomous and the variegated variants of the predominantly quadripartitous sculptural stage do not characterize two different species as the Canadian specimens exhibiting them occur together and intergrade. For example, these two extremes and a transitional variant are represented in the suite of 5 specimens collected by Kemper (1977, p. 3, Figure 3) from his bed 16.

The variegated variant of the quadripartitous stage appears distinctly earlier than does its bidichotomous variant. In the lectotype and the GSC Cat. 77108 it appears at least three-quarters of a whorl to one whorl (and possibly more) before the beginning of the adult living chamber. Furthermore, it appears at the lesser shell diameters ranging from 49 mm (Klimova, 1981, Pl. IX, fig. 4) to 74 mm (GSC Cat. 77096; Pl. 32, fig. 3). The bidichotomous variant appears either at the beginning of adult living chamber or just before it and at considerably larger shell diameters ranging from 75 to 95 mm (e.g. in GSC Cat. 77104; Pl. 37, fig. 2; GSC Cat. 77116; Pl. 44, fig. 3; and GSC Cat. 17244; Pl. 39, fig. 1). The meaning of these distinctions is uncertain.

Suture line. No juvenile external suture lines are available in the Canadian material. Such sutures were, apparently only published by Klimova (1981, p. 78, 79, Figures 3a, 3b). The most advanced suture published by Klimova (l. cit., Figure 3b) occurs on the fourth whorl from the protoconch. It still lacks clearly developed second and third auxiliary lobes and so is an early juvenile one.

The earliest sutures available in our material occur in the specimen GSC Cat. 77111 (Figure 52a) at the shell diameter of about 35 mm. They exhibit all three auxiliary lobes, which are arranged like those of the terminal suture lines (Figures 52b, 52c) and so are early adult by definition. These sutures are inferred to occur somewhere on the sixth whorl from the protoconch. Therefore, the external suture of *S.* (*S.*) *stubendorffi* appears to become adult at least three whorls before the oral end of the adult phragmocone.

The ventral lobe of the GSC Cat. 77111 suture is somewhat longer than and about as wide as its first lateral lobe. This slender (about 3.5 times longer than wide), subparallel-flanked lobe is rather simply and shallowly denticulated, except for the unusually long and slender apical prongs.

The first lateral saddle is up to 1.5 times wider than the ventral lobe and bears two simply notched first order lobules.

The moderately slender (about 3 times longer than wide) and parallel-sided first lateral lobe is simply and shallowly denticulated and subsymmetrically trifid.

The width of unusually narrow second lateral saddle is about three-quarters that of the first lateral lobe; its small first order lobules are only partly notched.

The slender (3 to 3.5 times longer than wide), parallel-sided to adapically tapering, and subsymmetrically bifid (mostly) to asymmetrically trifid second lateral lobe is situated on the mid-flank and is denticulated almost exclusively by simple, short lobules.

The unusually narrow third lateral saddle is either about as wide as the second lateral lobe or comprises only about three-quarters of its width. Its top bears only one simple notched lobule.

The rather slender (3.5 to 4 times longer than wide), subparallel-flanked to slightly adapically tapering first auxiliary lobe is situated in the adumbilical quarter of the flank. Its length is about three-quarters that of the second lateral lobe. This subsymmetrically trifid lobe is almost exclusively simply and shallowly denticulated.

The fourth lateral saddle is restricted to the adumbilicalmost part of the flank, except for the apicalmost suture where it extends onto the outermost part of the umbilical wall. This relatively widened saddle is 1 1/2 to almost 2 times wider than the first auxiliary lobe.

The second auxiliary lobe is shaped and proportioned like the first auxiliary, except for being more slender (its length/width ratio being 4 to 4.5). Its length is about 3/4 that of the first auxiliary and it is only simply notched. This lobe occupies most of the middle third of the umbilical wall in the apicalmost suture visible but moves to its

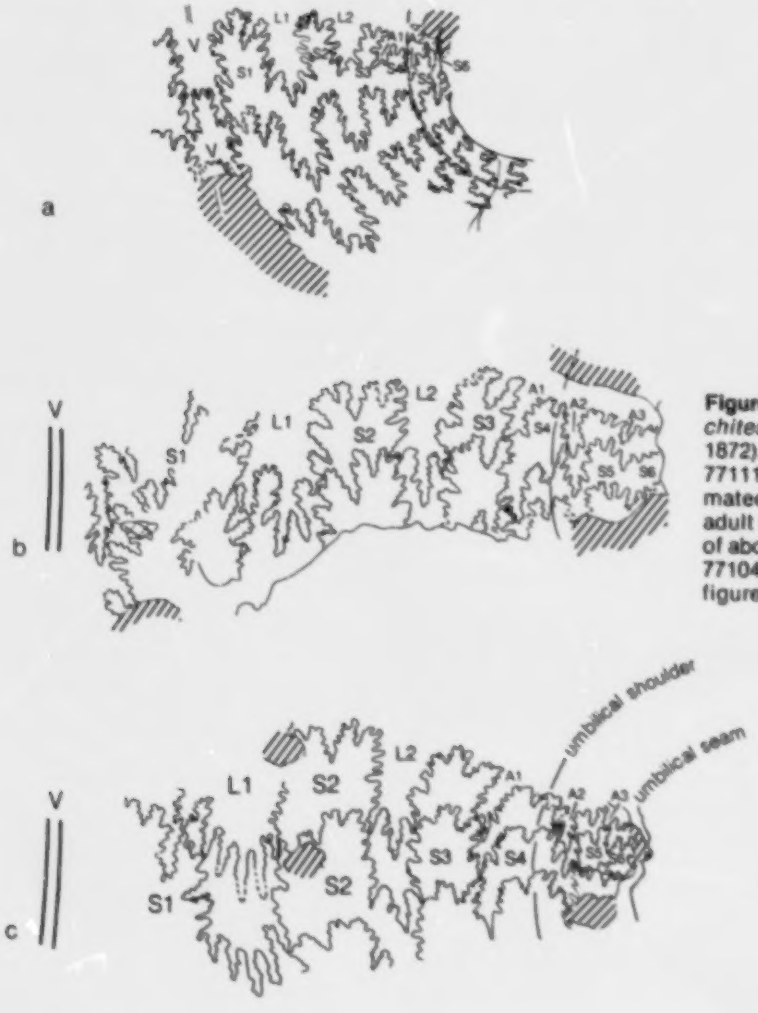


Figure 52. Adult external suture lines of *Siberiptychites (Siberiptychites) stubendorffi* (Schmidt, 1872). **a**. Early (?earliest) adult sutures. GSC Cat. 77111 at the shell diameter of about 35 mm (estimated 6th whorl from the protoconch); **b**. Terminal adult sutures. GSC Cat. 77116 at the shell diameter of about 75 mm; **c**. Terminal adult sutures. GSC Cat. 77104 at the shell diameter of about 76 mm. All figures approx. X1.

outermost part in the next five sutures (Figure 52a). This ontogenetic change is coupled with that of adjacent sutural elements described below.

The width of the fifth lateral saddle varies from two (mostly) to three (rarely) times that of the second auxiliary lobe. This sparcely and mostly simply denticulated saddle occupies most of the inner third of the umbilical wall in the apicalmost suture visible but moves adventrally into its middle part in the next five sutures (Figure 52a).

The slender and long (its length/width ratio is 3.5 to 4.5), subparallel-sided third auxiliary lobe has simply and shallowly notched flanks and a symmetrically to asymmetrically trifid tip. This lobe is positioned next to the umbilical seam in the earliest two sutures visible but gradually moves adventrally in the next four sutures. The outer part of the sixth lateral saddle appearing behind the lobe in these sutures gradually widens until its width becomes subequal to that of the lobe in the sixth suture.

The imaginary line connecting the tops of the saddles of these sutures is ascendant at 20 to 25 degrees through their lateral parts. Then it turns around gradually above the third lateral saddle into a subradial orientation which is then maintained to the umbilical seam (Pl. 64, fig. 2; Figure 52a).

Other well preserved and complete external sutures were observed only on the adult penultimate whorl. All these late adult to terminal sutures are considerably more complexly and deeply denticulated than the early adult suture of GSC Cat. 77111 (compare Figure 52a with 52b, 52c, 53a, and 53b). Their lobes are relatively more attenuated and separated by relatively widened saddles. These distinctions are particularly strongly expressed in the terminal sutures (Figures 52a, 52b) while the late adult sutures of GSC Cat. 77104 (Figures 53a, 53b) are morphologically intermediate.

These adult sutures are rather variable in most other morphological features. Their ventral lobe is mostly about as long as the first lateral lobe (e.g. GSC Cat. 77101; Pl. 36, fig. 1A, 1E; Figure 53a). However, it may be either somewhat shorter (e.g. GSC Cat. 77104: Pl. 37, fig. 2B; Figure 52c) or somewhat longer (e.g. GSC Cat. 77116;

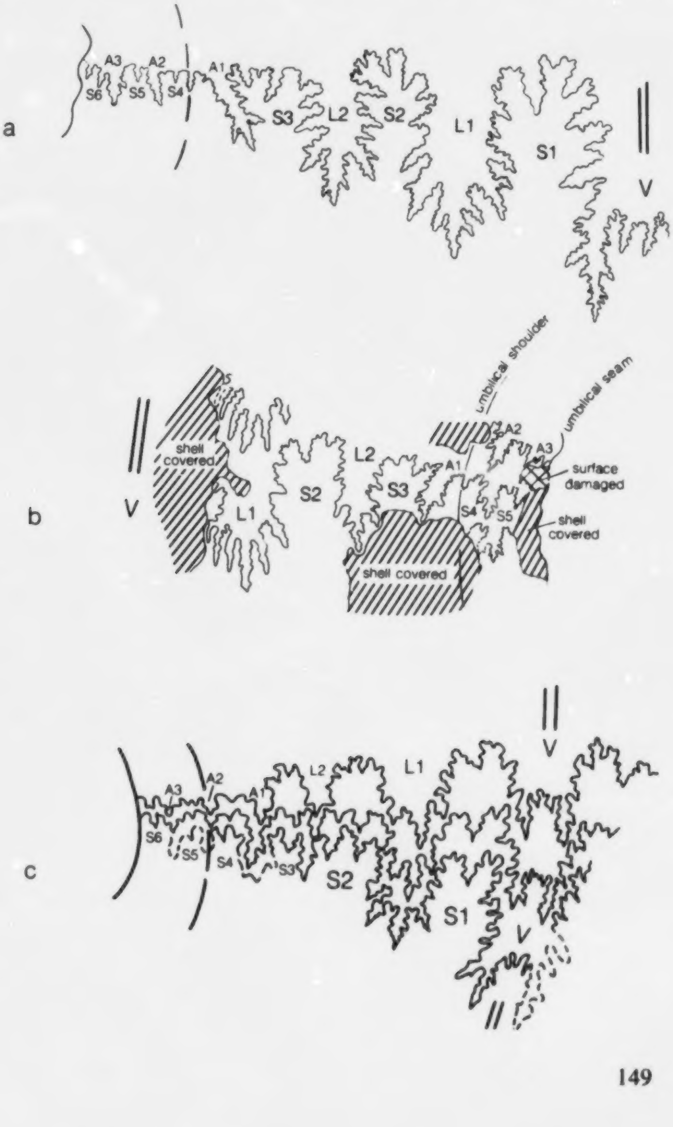


Figure 53. Adult external suture lines of *Siberiptychites* (*Siberiptychites*). **a.** *S.* (*S.*) *stubendorffi* (Schmidt, 1872). Earlier adult suture of the slender variant. Specimen GSC Cat. 77101 reproduced in Pl. 36, fig. 1 at the approx. shell diameter of 71 mm. **b.** *S.* (*S.*) *stubendorffi* (Schmidt, 1872). Earlier adult suture of the intermediate variant. Specimen GSC Cat. 77104 reproduced in Pl. 37, fig. 2 at the approx. shell diameter of 65 mm. **c.** *S.* (*S.*) n. sp. aff. *stubendorffi* (Schmidt, 1872). Terminal adult sutures of the specimen GSC Cat. 77103 reproduced in Pl. 37, fig. 1 at the approximate shell diameter of 93 mm. All figures X1 (approx.).

Pl. 54, fig. 1A; Figure 52b) than that lobe. The two are comparably strongly and deeply denticulated.

The first lateral saddle varies from about as wide as the ventral and the first lateral lobes (e.g. GSC Cat. 77101: Pl. 36, fig. 1B, 1E; Figure 53a) to almost twice as wide as either of them (e.g. GSC Cat. 77104; Pl. 37, fig. 2B; Figure 52c). In some advanced adult sutures (e.g. 77101; Figure 53a) this saddle is subdivided in three parts by two rather unequally-sized lobules. However, in the terminal sutures (e.g. GSC Cat. 77104; Figure 52c) it is subdivided in four parts by three lobules.

The first lateral lobe may be moderately slender (length/width ratio about 3), distinctly constricted at the top and markedly asymmetrically trifid (e.g. in GSC Cat. 77116; Pl. 44, fig. 3; Figure 52b) but it may be more slender (about 3.5 times longer than wide) subparallel-flanked and regularly trifid (e.g. GSC Cat. 77101: Pl. 36, fig. 1A, 1E; Figure 53a). It may also be slender and subparallel-flanked but with a five-pronged instead of trifid tip (e.g. GSC Cat. 77104; Pl. 37, fig. 2B; Figures 52c, 53b).

The width of the second lateral saddle varies within the same limits as that of the first lateral saddle. This saddle is relatively more narrow in the advanced adult sutures (e.g. GSC Cat. 77101 and 77104; Figures 53a, 53b) but widens and becomes more complexly denticulated at and near the end of adult penultimate whorl (GSC Cat. 77104 and 77116; Figures 52b, 52c).

The second lateral lobe is comparably simply and shallowly denticulated to the first lateral lobe but is relatively sturdier (length/width ratio of 2 1/2 to 3 1/2) with its sturdiest examples occurring in the sturdy variant of the species (e.g. GSC Cat. 77115; Pl. 44, fig. 1A). It is always subparallel-sided and symmetrically to markedly asymmetrically trifid.

The relatively more deeply and complexly denticulated third lateral saddle is situated on the addorsal part of the flank. It is from 1 1/2 times (e.g. GSC Cat. 77101; Pl. 36, figs. 1A, 1E; Figure 53a) to 2 times (e.g. GSC Cat. 77104; Pl. 37, fig. 2B; Figures 52c, 53b) wider than the second lateral lobe and either not wider (e.g. GSC Cat. 77116; Figure 52b) or up to 1 1/2 times (e.g. GSC Cat. 77101; Figure 53a) wider than the second lateral saddle.

The rather slender (the length/width ratio of about 5; e.g. GSC Cat. 77101; Pl. 36, fig. 1A, 1C; Figure 53a), symmetrically to asymmetrically trifid first auxiliary lobe is always situated on the adumbilicalmost flank. Its length fluctuates from two-thirds to three-quarters that of the second lateral lobe and the flanks are only sparcely and shallowly denticulated. Unlike all other lobes, this lobe is invariably inclined adventrally at 20 to 40 degrees.

The fourth lateral saddle always extends over the innermost flank and the outermost umbilical wall (Figures 52b, 52c, 53b). It is either about as wide as or somewhat more narrow than the third lateral saddle and is considerably more simply and shallowly denticulated.

The second auxiliary lobe is always situated on the outer part of the umbilical wall (Pl. 36, fig. 1E; Pl. 37, fig. 2B; Figures 52b, 52c, 53a, 53b). The length of this pronouncedly asymmetrically trifid lobe is about three-quarters that of the first auxiliary lobe and it is appreciably less slender than the latter (the length/width ratio of 4 or less).

The relatively narrowed fifth lateral saddle, which occupies the mid-umbilical wall, may be only slightly wider than the second auxiliary lobe (e.g. GSC Cat. 77101; Pl. 36, fig. 1E). However, it may be more than two times wider than that lobe (e.g. GSC Cat. 77104; Figures 52c, 53b). This saddle is only sparcely and simply denticulated.

The third and last auxiliary lobe is situated on the inner part of the umbilical wall and measures from one-third to one-half the length of the second auxiliary lobe. This appreciably adapically tapering lobe is indistinctly trifid and only slightly notched on the flanks. The length/width ratio of this sturdy structure is only 2 in the sturdy variant of the species (e.g. GSC Cat. 77116) but it increases somewhat in the intermediate and slender variants (e.g. Pl. 36, fig. 1E; Figures 52c, 53b).

A greater part of the only slightly and sparcely notched sixth lateral saddle is always exposed between the third auxiliary lobe and the umbilical seam (e.g. Pl. 36, fig. 1E; Figure 53a). No part of the fourth auxiliary lobe was observed in the material studied.

The lateral parts of all late adult to terminal external sutures are slightly to distinctly ascendant while their auxiliary parts, beginning with the first auxiliary lobe, are either subradially oriented (e.g. Figure 52c) or slightly to distinctly descendant (Pl. 36, fig. 1E; Figure 53a).

The late adult external suture of the lectotype of *S.* (*S.*) *stubendorffi* (Pavlow, 1914, p. 32, Pl. VI, fig. 1c) differs from the above described equivalent Canadian sutures (compare Figures 52b, 52c, 53a, 53b) in a relatively lesser width of all its lateral saddles which are either about as wide as the preceding lobes or somewhat more narrow than they (e.g. the second lateral saddle). Only the first and second lateral saddles of the GSC Cat. 77101 (Figure 53a) are similarly wide to the equivalent saddles of the lectotype. However, its third to sixth lateral saddles are either as wide or wider than the equivalent saddles of other Canadian sutures. The relative width of the saddles of the lectotype is also similar to that of the equivalent saddles in the early (?earliest) adult external suture of GSC Cat. 77111 (Figure 52a).

Though somewhat scanty, the above data indicate that the relative width of the lateral saddles varies within rather wide limits. The ontogenetic and taxonomic implications of this variation shall be discussed below in the description of the external suture of *S.* (*P.*) *middendorffi* (see p. 169, 170).

Affinities and differences. The morphological distinctions of *S.* (*S.*) *stubendorffi* from *S.* (*S.*) n. sp. aff. *stubendorffi* and *S.* (*S.*) *fascicostatus* are discussed in the description of these forms.

Stratigraphic relationships, geographic distribution and age. *Siberiptychites* (*Siberiptychites*) *stubendorffi* is a widespread high Boreal species, which was already known to occur in East Greenland and several regions of northern Siberia (see in the synonymy and in Saks et al., 1963, p. 179-181) prior to its discovery in the upper Deer Bay Formation of the Sverdrup Basin. The species was recently found in Spitsbergen, where its presence was already suggested on the basis of a morphologically similar but not firmly identifiable specimen described and figured as *Polyptychites* aff. *ramulicosta* by Frebold (1929, see in the synonymy).

The Spitsbergen polyptychitinid identified and figured as *Polyptychites* aff. *ramulicosta* by Yershova (1980, p. 71, Pl. VI, fig. 2) is a rather typical advanced whorl of the sturdy variety of *S.* (*S.*) *stubendorffi*. This is indicated by the presence of well developed constrictions in the figured specimen (e.g. Pl. VI, fig. 2a) combined with the absence of *Astieriptychites*-like flexuosity and forward inclination of its apparently trivirgatitpartituous and quadrivirgatitpartitous rib bundles and the slight development of its apparently but slightly incurved bullate primary ribs. The secondary ribs of this specimen are but slightly and very broadly forward convex on the venter, as it is typical of *S.* (*S.*) *stubendorffi*. This occurrence of *S.* (*S.*) *stubendorffi* dates the regional "*Polyptychites ramulicosta*" Zone of Yershova (1980, p. 70, 71) as of the late early Valanginian age and equates it with part or all of the *Polyptychites michalskii* Zone of North Siberia.

In the Sverdrup Basin most of the representatives of *S.* (*S.*) *stubendorffi* were found by Kemper (1977, p. 3, Figure 3) on Amund Ringnes Island in bed 16 (GSC loc. 91310) of his section 11 situated about 249 m stratigraphically below the top of the Deer Bay Formation and about 24 m stratigraphically below bed 14. The latter yielded the youngest, presumably specifically different, representatives of *Siberiptychites*.

Two more specimens of *S.* (*S.*) *stubendorffi* were found in bed 17 of the above section (GSC locs. 91311 and 93760); which is situated slightly below bed 16. They are associated with a solitary specimen of *S.* (*P.*) cf. or aff. *middendorffi* (Pavlow, 1914).

Another important locality for *S.* (*S.*) *stubendorffi* is GSC loc. 37867 on Ellef Ringnes Island, N.W.T. situated on the north bank of the delta of a nameless creek at a point 1 7/8 mile east of the Isachsen Weather Station. Its stratigraphic level below the Deer Bay-Isachsen contact is uncertain, but is believed to be in order of 91 to 106 metres (300 to 350 feet). One specimen of a sturdy variant was found here associated with one specimen of the sturdy variety of *S.* (*P.*) *middendorffi*, one *S.* (*S.*) *fascicostatus* and several *Buchia sublaevis* (Keyserling) (Jeletzky, 1964, p. 22).

A solitary representative of *S.* (*S.*) *stubendorffi* from GSC loc. 91354 on Ellesmere Island, N.W.T. (Reptile Creek, at a point 1.5 mi N from the airport of Eureka Weather Station, appr. Lat. 80°00'18"N; Long. 85°52'W) was found on the float of the upper Deer Bay Formation in association with *Astieriptychites* sp. indet. A. According to E. Kemper (personal communication of August 1974) these ammonites were found at a level assumed to be only about 60 m stratigraphically below the base of the Isachsen Formation.

Only Kemper's (1977, p. 3, Figure 3) section on Amund Ringnes Island provides information about the relationship of the *Siberiptychites* (*Siberiptychites*) *stubendorffi*-bearing beds with those containing other biochronologically significant ammonite faunas and hence about their age in terms of the European standard zones and international standard stages. In this section the *S.* (*S.*) *stubendorffi* fauna is overlain by the *S.* (*S.*) n. sp. aff. *stubendorffi* fauna which is also known at the better datable GSC loc. 82695. For reasons presented in the description of *S.* (*S.*) n. sp. aff. *stubendorffi*, this fauna appears to be only slightly younger than *S.* (*S.*) *stubendorffi* fauna proper. The two are considered herein tentatively as subdivisions of the same generalized *Siberiptychites* Beds (Figure 62).

The unfortunately poorly documented fossil beds (see p. 119, 120 and 156) of the GSC loc. 82695 are inferred to be younger than Kemper's (l. cit.) beds 17 and 16 containing the *S.* (*S.*) *stubendorffi* fauna proper. These latter beds and the older *Polyptychites keyserlingi*-*S.* (*S.*) n. sp. aff. *stubendorffi* fauna of GSC loc. 82695 are correlated respectively with the upper lower and lower upper parts of the *Polyptychites michalskii* Zone of northern U.S.S.R. Taken together, they correspond to the middle part of the so called *Polyptychites* Beds of Northwest Germany (Figure 62). They are, accordingly, of late, but not latest, early Valanginian age. This assignment of the *S.* (*S.*) *stubendorffi*- and *P. keyserlingi*-bearing beds of the Sverdrup Basin agrees well with their direct superposition first on those containing the *Thorsteinssonoceras ellesmerense* fauna and then on those containing the *Temnoptychites* (*Temnoptychites*) *kemperi* fauna (Kemper, 1977, p. 3, Figure 3; Jeletzky, 1979, p. 56-58, Text-fig. 8). The two latter sequences of beds appear to be correlative respectively with the lower lower part of the *Polyptychites michalskii* Zone and the upper subzone of the *Temnoptychites* (*Temnoptychites*) *syzranicus* Zone of North Siberia. In Northwest Europe these two Sverdrup Basin faunas appear to correspond respectively to the *Polyptychites pavlowi* Zone and the *Platylenticeras* (s. lato) *involutum* Zone of the early, but not the earliest, early Valanginian.

Other Sverdrup Basin localities of the *Siberiptychites* (*Siberiptychites*) *stubendorffi* fauna do not provide any stratigraphical and age information as their stratigraphic relationships with any older or younger, biochronologically significant Valanginian ammonite faunas remain obscure. The association of *S.* (*S.*) *stubendorffi* with *Astieriptychites* sp. indet. A at GSC loc. 91354 does not help as the time range of *Astieriptychites* in northern Siberia remains in doubt (Gol'bert et al., 1981, p. 56-59, Tables 4, 14).

The above defined, rather narrow time range of the *Siberiptychites* (*Siberiptychites*) *stubendorffi* fauna in the

Sverdrup Basin conflicts with its considerably wider time range (i.e. from the *Temnoptychites simplicissimus* Subzone of *Temnoptychites syzranicus* Zone to the top of the *Polyptychites michalskii* Zone inclusive; Figure 62) in northern Siberia (Jeletzky, 1973, p. 66, 67, Figure 3; 1979, p. 56-58, Text-fig. 8; Kemper, 1977, p. 4, Figure 3; Klimova, 1978, p. 530; Gol'bert et al., 1981, p. 56, 59, Table 14). According to Kemper (1977, p. 4): "This contradiction must reflect either different concept of taxa employed by Russian workers or the condensation of index fossils of two or more adjacent zones in thin beds of their more attenuated sequences". However, Jeletzky (1979, p. 58) preferred to explain these differences in time ranges by invoking gradual interregional migrations of diagnostic Valanginian ammonites within the Boreal Realm. This idea was also introduced by Kemper (1977, p. 5, Figure 2) but not applied to this particular situation. According to this interpretation, which is now favoured by the writers and is here discussed in a greater detail in the description of subgenus *Siberiptychites*, *S.* (*S.*) ex gr. *stubendorffi* arose in Northern Siberia from the genus *Bodylevskites* early in the time range of *Temnoptychites* (*Temnoptychites*) *syzranicus*. Thereafter these forms migrated gradually eastward until they reached the Sverdrup Basin shortly after the next following *Thorsteinssonoceras ellesmerense* time (Figure 62). Furthermore, *S.* (*S.*) ex gr. *stubendorffi* must have disappeared in the Sverdrup Basin well before the end of *Polyptychites michalskii* time while it continued to exist to its end in North Siberia.

The presence of *S.* (*S.*) *stubendorffi* in the rather peculiar, possibly condensed, but presumably late early to mid-early Valanginian *Polyptychites* s. str. etc. fauna of Trail Island, eastern Greenland (Jeletzky, 1973, p. 67; 1979, p. 58) could reflect its similar westwardly directed interregional migration from the North Siberian evolutionary center. The same may be true of its occurrence in the equivalents of the *Polyptychites michalskii* Zone on Spitsbergen (Frebold, 1929; Yershova, 1980, p. 71, Pl. VI, fig. 2).

Siberiptychites (*Siberiptychites*) n. sp. aff. *stubendorffi* (Schmidt, 1872)

Pl. 33, fig. 2; Pl. 37, fig. 1; Pl. 38, fig. 1; Pl. 42, fig. 1; Pl. 62, fig. 1; Pl. 63, fig. 2; Figures 53c, 54c.

Material. Five fragmentary to almost complete specimens from GSC localities 91308, C-4749, 93754 and 82695 in Sverdrup Basin.

Diagnosis. Medium-sized *Siberiptychites* (*Siberiptychites*) species which differs from *S.* (*S.*) *stubendorffi* in the rounded-rectangular, distinctly subtrapezoidal (adventrally narrowing) cross-section of its intermediate and advanced whorls and the replacement of the predominantly trivirgatitpartitous sculpture of earlier advanced whorls by predominantly trifasciculate to quadrifasciculate bundles on the last two whorls of the phragmocone.

Measurements in mm

Specimen	Shell diameter	Umbilicus (per cent)	wh 1	wh 2	wth 1	wth 2
GSC Cat. 77103	95	21 (22)	41(43)	31(35)	51	41

Description

Whorl shape and proportions. The specimen GSC Cat. 77109, which offers almost undistorted cross-sections of six early to intermediate whorls beginning with the initial one (Pl. 42, fig. 1), indicates that the characteristic rounded-rectangular, adventrally narrowing cross-section of this form first appears at a shell diameter of about 20 mm. The earlier whorls exhibit a complex sequence of typically *Siberiptychites*-like cross-sections indistinguishable from those of equivalent whorls of *S.* (*S.*) *stubendorffi* (see the description of *Siberiptychites* for further details).

The flanks of subsequent intermediate and adult whorls (Pl. 37, fig. 1, Pl. 38, fig. 1; Pl. 42, fig. 1; Pl. 63, fig. 2C; Figure 54c) are straight to but slightly convex. From their largest width at the level of the umbilical shoulder the flanks converge evenly but slightly (i.e. at about 10 degrees) all the way up to the broadly rounded but distinct ventral shoulder where they merge into a broad, only slightly arched venter. Addorsally, the flanks merge rapidly into a straight to only slightly convex umbilical wall across a narrowly rounded umbilical shoulder. The umbilical wall is oriented approximately perpendicular to the shell's plane of symmetry (Pl. 42, fig. 1; Figure 54c). The moderately involute (20 to 22 per cent), deep umbilicus is almost regularly funnel-like as the preceding whorls are covered almost to the umbilical shoulder (for 85 to 90 per cent).

Sculpture. The end phase of the *Bodylevskites*-like sculptural stage (*see* p. 136, 137) is the earliest observed; it is exposed in the whorl fragment GSC Cat. 77106 (Pl. 38, figs. 1C-1F) which corresponds to the shell diameter of about 27 mm. This fragment exhibits two trivirgatitpartitous rib bundles typical of the stage which are followed by two simple dichotomous bundles presumably marking the beginning of the simple dichotomous sculptural stage. On this segment the fine, closely spaced primaries begin in the proximity of the umbilical seam. They extend across the regularly rounded umbilical shoulder and the lower one-quarter to one-third of the flank before bifurcating (Pl. 38, figs. 1C, 1D). These primary ribs gradually become more and more prominent all the way to their branching point without becoming thickened. They are all distinctly inclined forward and approximately straight, except immediately below the branching point where they bend comma-like forward. They are all low and round-topped, being internal casts. The supplementary ribs are appreciably more refined and closely spaced than the primary ribs. They are somewhat stronger inclined forward on the flank's middle and this inclination gradually increases all the way to the mid-venter where the ribs turn around to join the supplementary ribs of the other flank.

The ribs are neither interrupted nor weakened on the venter and their marked but broad bends there have a slightly angular appearance because of an almost complete absence of a sinuosity (Pl. 38, fig. 1E). All supplementaries observed are internal casts and so are low and roundtopped. However, some rather small fragments of shell-covered ribs are sharptopped and wedge-like in cross-section.

The bulk of the simple dichotomous sculptural stage was observed only on the earliest preserved one-third of the whorl of the badly deformed specimen GSC Cat. 77098 (Pl. 33, fig. 2B). Its sculpture does not appear to differ materially from its above described example and from the better preserved examples observed in *S.* (*S.*) *stubendorffi* and *S.* (*P.*) *middendorffi* (see there for further details). The sculpture of the subsequent one and a half whorls between the approximate shell diameters of 35 to 45 mm is also observable in this badly deformed specimen (Pl. 33, fig. 2A). This interval appears to be ornamented largely or ?entirely by trivirgatitpartitous bundles representing the early phase of the predominantly trivirgatitpartitous sculptural stage. The sculpture of this phase does not differ materially from the late trivirgatitpartitous sculpture exposed in the somewhat larger, presumably next subsequent whorl of the GSC Cat. 77106 and described below.

The halfwhorl of the GSC Cat. 77106 beginning at the estimated shell diameter of 46 mm (Pl. 38, fig. 1A, 1B) is still dominated by the trivirgatitpartitous bundles and so represents this sculptural stage. Some solitary, single or dichotomous ribs restricted to the middle and upper flanks are intercalated between these bundles. The slender primaries are restricted to the outer half of the umbilical wall and the lowermost one-sixth to one-fifth of the flank. They are distinctly elevated just above the umbilical shoulder and so are bullae rather than primary ribs. These bullae are roundtopped whenever preserved as internal casts but are sharp-topped and wedge-shaped in those rare instances when they are shell-covered. The supplementary ribs are invariably weathered and appear to be low and roundtopped, regardless of the presence or absence of the shell layer. They are only slightly flexuous while being distinctly to markedly inclined forward on the flank. The anterior rib of every bundle is the most strongly inclined while its posterior rib is the least inclined. The forward bends of all supplementary ribs increase distinctly on the ventral shoulder. Thereafter they form marked but broad forward bends on the venter which appear to be somewhat stronger expressed than those on the inner whorl of the specimen. The end part of the trivirgatitpartitous stage is not represented in our material, except possibly in the specimen GSC Cat. 77136 (see below).

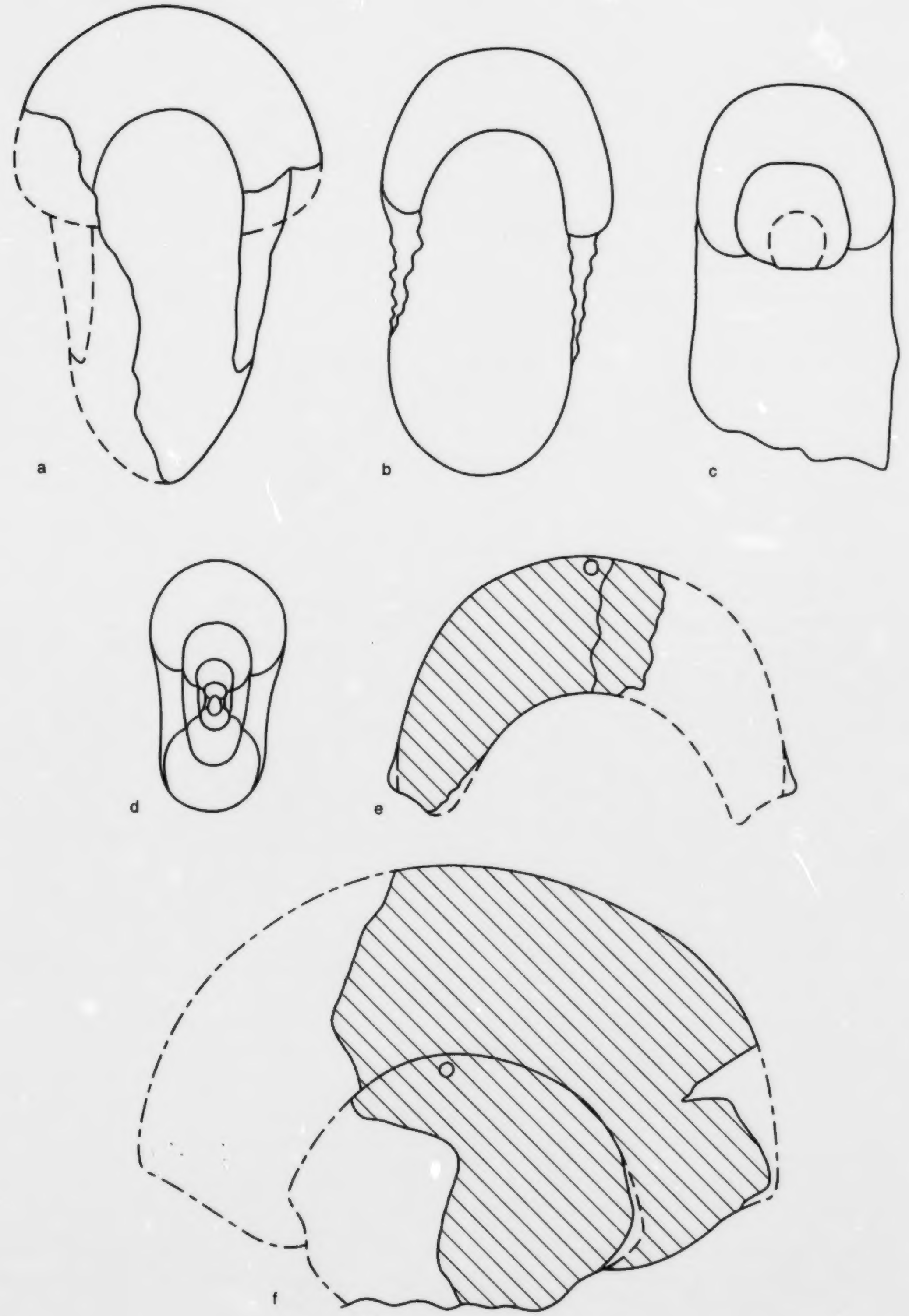
The lower parts of primary ribs of two preceding whorls visible in the umbilicus of the GSC Cat. 77103 (Pl. 37, fig. 1A) appear to represent the late trivirgatitpartitous stage, in part at least. They are similar to the primaries of GSC Cat. 77106 and 77136, except that they begin at the umbilical seam, which may reflect their better preservation. There are 25 primaries on the last of these two whorls and either 25 or 26 primaries on the preceding whorl.

The predominantly fasciculate variant of the next older, predominantly quadripartitous sculptural stage (see p. 138, 139) was observed in the specimens GSC Cat. 77136 (Pl. 62, fig. 1; Pl. 63, fig. 2), 77106 (Pl. 38, fig. 1A), 77103 (Pl. 37, fig. 1), and an unfigured specimen from GSC loc. C-4749. Its early part is best displayed in the well preserved, apparently undeformed last whorl fragment of the GSC Cat. 77136. This nonseptate fragment represents a living chamber which appears to be an intermediate one (another possibility is that this specimen is a micromorph) because it is only 30 mm high and 33.5 mm wide at the oral end. This contrasts with the GSC Cat. 77103 (Pl. 37, fig. 1A, 1B) where the adult living chamber, recognizable because of a marked crowding and simplification of the terminal suture lines combined with a farreaching weakening of the sculpture, begins at the whorl's diameter of about 45 mm.

The specimen GSC Cat. 77136 is ornamented almost exclusively by well formed quadri- to tri-fasciculate rib bundles. Only one or two trivirgatitpartitous bundles occur at its apical end where they flank a well developed constriction and where the sculptural pattern is considerably disorganized (Pl. 62, fig. 1; Pl. 63, fig. 2A). The slender and low primary ribs, which give naissance to these bundles, begin within the outer half of the umbilical wall and extend across the umbilical shoulder and the lowermost quarter of the flank. They are about twice as thick and high as the secondaries, are bent backward on the umbilical wall but turn forward gradually on the umbilical shoulder and flank acquiring a forward concave, comma-like shape. The ribs do not seem to be swollen anywhere but are slightly elevated on the umbilical shoulder and so may be designated as slightly bullate primaries. They are all preserved as internal casts only. The better preserved right flank exhibits about 8 of these primaries, which prorates to some 24 to 26 per whorl. The primaries are separated by roundbottomed, concave interspaces which are about 2 1/2 times wider than they on the apical part of the fragment and 3 to 3 1/2 times wider than they on its oral part.

All three secondaries are firmly attached to their primary rib in the trifurcate fasciculate bundles. However, in the quadrifasciculate bundles the posterior secondary is only indistinctly attached to its primary rib. Only one undivided intercalated secondary rib restricted to the middle and upper flank was observed. The secondaries are somewhat deflected backward initially in relation to the direction of their primaries. Then they become distinctly forward inclined while being approximately straight to but slightly forward convex and retain this orientation throughout the rest of the flank. Their forward inclination increases slightly on the ventral shoulder and they form gentle and broad forward arches across the broad, almost flat venter (Pl. 63, fig. 2B).

This early phase appears to be represented also in the short fragment of the last whorl of GSC Cat. 77106 (Pl. 38, fig. 1A) which appears to be ornamented by the


a
b
c
d
e
f

fasciculate rib bundles. The same is, finally, true of the unfigured fragment from GSC loc. C-4749 representing the beginning of an apparently intermediate living chamber with the last suture line still visible. This fragment is only 29 mm high and 30 mm wide at its oral end.

The later part of the quadripartitous sculptural stage is exposed on the last preserved whorl of the only known adult representative of *S.* (*S.*) n. sp. aff. *stubendorffi* (GSC Cat. 77103; Pl. 37, fig. 1A), which includes the apicalmost part of the living chamber and has a terminal shell diameter of about 100 mm. The complete shell must have had a diameter of 140 to 150 mm. It is an adult because the last few of its sutures are strongly simplified and crowded (Pl. 37, fig. 1A, 1B; Figure 53c). Furthermore, the sculpture is at first strongly weakened and then almost lost on the oral two-thirds of this whorl between the illdelimited bullate primaries on the umbilical shoulder and the still discernible, albeit low and roundtopped, supplementaries on the umbilical rounding. These morphological changes are quite obvious in spite of an appreciably to markedly weathered state of the whorl.

The earliest exposed third of the whorl is ornamented by an alternation of quadrifasciculate to trifasciculate rib bundles with subordinate tri- and quadri-virgatitpartitous bundles. The spacing, orientation, and general appearance of these primary and secondary ribs are similar to those of the previously discussed specimens GSC Cat. 77136 and 77106, except for an already noticeable weakening of the sculpture on the mid-flank. The feebly bullate primaries are similar to those of the previously discussed earlier two whorls.

The sculpture of the remaining two-thirds of the whorl is too strongly weakened on the flanks to be certain of the bundling habit, except that some of the bundles at least seem to be either three- or quadri-fasciculate. The spacing, orientation, and general appearance of the supplementaries on the flank do not appear to differ materially from those of the early third of the whorl, except for that weakening. However, they become distinctly more coarse and more sparce on the venter. The bullate primaries become more sparce and more prominent and are restricted to the lowermost part of the flank. There are only about 18 bullate primaries on the entire whorl and 52 or 53 supplementary ribs were counted on its early half. Two feebly impressed constrictions, which follow the course of adjacent ribs, occur on the whorl.

Figure 54. Whorl cross-sections of *Siberiptychites* species. **a**. Sturdy variant of *Siberiptychites* (*Siberiptychites*) *stubendorffi* (GSC Cat. 77115); **b**. Slender variant of *S.* (*S.*) *stubendorffi* (GSC Cat. 77101); **c**. *S.* (*S.*) n. sp. aff. *stubendorffi* (GSC Cat. 77103); **d**. *S.* (*Pseudoeuryptychites*) *middendorffi* (GSC Cat. 77100). Juvenile to early intermediate whorls; **e**. *S.* (*P.*) cf. or aff. *middendorffi* (GSC Cat. 77137). Posterior cross-section (Pl. 66, fig. 1A). **f**. *Siberiptychites* (*Pseudoeuryptychites*) n. sp. indet. A (GSC Cat. 77119). Adult ultimate and penultimate whorls. All figures X1.

Suture line. The adult external suture line was only observed on the intermediate (?third adult penultimate) whorl of specimen GSC Cat. 77098 (Pl. 33, fig. 2A) and on the last three-quarter whorl of the phragmocone of adult specimen GSC Cat. 77103 (Pl. 37, fig. 1A; Figure 53c). The former suture is about equivalent to the early (?earliest) adult suture of specimen GSC Cat. 77111 of *S.* (*S.*) *stubendorffi* (Pl. 64, fig. 2; Figure 52a). Like the latter suture, its second and third auxiliaries and its fourth and fifth lateral saddles are fully developed. Its third auxiliary is similarly situated exactly at the umbilical seam, so that no part of the sixth lateral saddle is exposed. This imperfectly preserved suture appears to differ from that of specimen GSC Cat. 77111 only in its relatively much more slender and long first lateral lobe, which is about 5 times longer than it is wide (Pl. 33, fig. 2A).

The only partly exposed (mostly lateral and ventral parts only) advanced adult sutures observed on the middle part of the specimen GSC Cat. 77103 (Pl. 37, fig. 1A) do not seem to differ in any respect from the corresponding parts of equivalent suture lines of *S.* (*S.*) *stubendorffi* (e.g. Figure 53a). However, its completely exposed but mostly more or less deeply weathered last few external sutures are strongly crowded and correspondingly shortened; they differ in the positioning of the two lateral and the first and second auxiliary lobes on the shell's flank where the second small, distinctly trifid auxiliary lobe is invariably situated on its adumbilicalmost part. Only the still smaller and sturdier, simple to slightly notched third auxiliary is situated in the middle of the umbilical wall. The third auxiliary is separated from the second auxiliary by a rather wide, flat topped fifth lateral saddle that occupies all of the umbilical shoulder and the outer half of the umbilical wall and is ornamented by three tiny and simple lobules. The third auxiliary is separated from the umbilical seam by the similarly wide outer part of the sixth lateral saddle which is subdivided into three parts by two tiny lobules. The more adventral of these is larger than the other and exhibits a suggestion of a trifid tip. No trace of the fourth auxiliary lobe was seen at the umbilical seam. All presently known advanced adult and terminal external sutures of *S.* (*S.*) *stubendorffi* (Figures 52b, 52c, 53a, 53b) differ in their second auxiliary lobe being situated on the outer part of the umbilical wall. Only in the early (?earliest) adult suture of GSC Cat. 77111 (Figure 52a) is that lobe situated on the crest of the umbilical shoulder.

The taxonomic value of these distinctions of the last adult sutures of *S.* (*S.*) n. sp. aff. *stubendorffi* remains uncertain, pending the study of more numerous and better preserved material. At any rate, the adventral migration of the second auxiliary lobe in specimen GSC Cat. 77103 takes place within the last quarter-whorl of its phragmocone. This lobe is definitely situated on the outermost part of the umbilical wall in the earlier suture lines.

Affinities and differences. S. (S.) n. sp. aff. *stubendorffi* differs from *S.* (*S.*) *stubendorffi* in:

1. The rounded-trapezoidal (i.e. adventrally contracting) cross-section of its intermediate and adult whorls; and
2. The replacement of predominantly trivirgatitpartitous bundling habit of the intermediate whorls by a predominantly fasciculated variant of the quadripartitous habit on the second before last and penultimate adult whorls immediately preceding the final feebly sculptured stage. The two outermost preserved whorls of *S.* (*S.*) *stubendorffi*, which succeed immediately those whorls bearing the trivirgatitpartitous ornament, exhibit, in contrast, a variant of the predominantly quadripartitous bundling habit where fasciculate rib bundles are either absent or scarce.

Furthermore, *S.* (*S.*) n. sp. aff. *stubendorffi* is not known to include any sturdy and low-whorled forms comparable to the sturdy variant of *S.* (*S.*) *stubendorffi*. However, this distinction may reflect simply the scarcity of material presently available.

S. (*S.*) n. sp. aff. *stubendorffi* differs from *S.* (*S.*) *fascicostatus* in its considerably more sturdy and wide, always wider than high, whorl shape and proportions and the replacement of the predominantly trivirgatitpartitous bundling habit of its intermediate whorls by a predominantly fasciculate ribbing habit on the late whorls. The latter habit appears already on the intermediate whorls of *S.* (*S.*) *fascicostatus*. Furthermore, the suture of *S.* (*S.*) n. sp. aff. *stubendorffi* has only three auxiliary lobes throughout its ontogeny. In *S.* (*S.*) *fascicostatus*, in contrast, a fourth auxiliary lobe appears already on the intermediate whorls.

From *S.* (*S.*) *mirus* (Voronets, 1962) *S.* (*S.*) n. sp. aff. *stubendorffi* differs first of all in the considerably lower and sturdier whorl proportions and the rounded-rectangular whorl cross-section. *S.* (*S.*) *mirus* has a higher, discoidally shaped whorl cross-section with a somewhat narrowly arched venter. Furthermore, it has a considerably wider, distinctly step-like umbilicus (Voronets, 1962, p. 69; Pl. XLI, fig. 3a). Finally, *S.* (*S.*) *mirus* is reported to exhibit a largely quasibidichotomous bundling habit (Voronets, 1962, p. 69).

The morphological distinctions of *S.* (*S.*) n. sp. aff. *stubendorffi* from all other *Siberiptychites* strongly suggest its being a new species. This conclusion finds further support in the apparent restriction of *S.* (*S.*) n. sp. aff. *stubendorffi* to beds younger than those in which *S.* (*S.*) *stubendorffi* was found (see below). Because of its morphology and stratigraphic position, the writers are inclined to interpret *S.* (*S.*) n. sp. aff. *stubendorffi* as a direct descendant of the slender variant of *S.* (*S.*) *stubendorffi*, which may develop a slightly angular whorl section (e.g. Pl. 36, fig. 1C; Figure 54b). However, *S.* (*S.*) n. sp. aff. *stubendorffi* could also be derived from such more slender and at the same time more *Astieriptychites*-like representatives of *Siberiptychites* as *S.* (*S.*) *fascicostatus* and *S.* (*S.*) *mirus*.

S. (*S.*) n. sp. aff. *stubendorffi* is left in open nomenclature pending the discovery of better material. All representatives presently available, including the almost complete adult shell GSC Cat. 77103, are judged to be unsuitable to serve as a holotype.

Stratigraphic relations and age. *S.* (*S.*) n. sp. aff. *stubendorffi* is only known from the Sverdrup Basin.

The three specimens of *S.* (*S.*) n. sp. aff. *stubendorffi* collected on Amund Ringnes Island, N.W.T. by Kemper (1977, p. 3, Figure 3) were found in concretionary bed 14 of his section 11 (i.e. GSC locs. 91308 and 93754) situated about 225 m stratigraphically below the top of the Deer Bay Formation and about 24 m stratigraphically above bed 16, which contains the last representatives of *S.* (*S.*) *stubendorffi*.

Of the other two *S.* (*S.*) n. sp. aff. *stubendorffi*, the unfigured specimen C-4749/2 was found by geologists of the Panarctic Oil Co. in 1969 on Axel Heiberg Island, N.W.T., west of Gibs Fiord, Princess Margaret Range at the Lat. 79°51'N; Long. 90°W. This specimen is recorded as derived from the middle to upper part of the Deer Bay Formation at a level 2305-2322 feet below the top of a measured section. The specimen GSC Cat. 77099 of *S.* (*P.*) *middendorffi* reproduced in Pl. 34, figs. 2A, 2B also forms part of that collection.

The second of these specimens GSC Cat. 77106 is from GSC Cat. 82695 (Pl. 42, fig. 1; Pl. 38, fig. 1). It was collected by the pilot of R. Thorsteinsson's field party in 1968 near the north tip of Amund Ringnes Island, N.W.T. from some part of the Deer Bay Formation (exact locality and stratigraphic level unknown). This specimen is believed to have been originally associated with *Polyptychites keyserlingi* in a bed equivalent to the bed 14 of the section 11 of Kemper (1977, p. 3, Fig. 3). Its apparent association with *P.* aff. *hapkei* and *P.* aff. *tschekanovskii* at GSC loc. 82695 is ascribed to an indiscriminate collecting of fossils from several stratigraphic levels.

The external correlation and age of the *S.* (*S.*) n. sp. aff. *stubendorffi*-bearing beds of the Deer Bay Formation were discussed on pp. 119, 120.

Judging by its representatives collected on Amund Ringnes Island by Kemper (1977, p. 3, Figure 3), *S.* (*S.*) n. sp. aff. *stubendorffi* is confined to the topmost part of the range of the subgenus *Siberiptychites* in the Sverdrup Basin. Therefore, it seems possible that its horizon represents a separate subzone (or even a new zone) within the *Siberiptychites* beds. However, much additional collecting elsewhere in the basin is needed to either confirm or reject this suggestion.

Siberiptychites (*Siberiptychites*) *fascicostatus* sp. nov.

Pl. 35, fig. 2; Pl. 39, fig. 2; Pl. 61, fig. 1; Figure 55a

Synonymy

1964 *Polyptychites*? cf. *densicosta* Jeletzky, p. 46, Pl. IX, figs. 5a-5c.
1969 *Polyptychites*? cf. *P.*? *densicosta* Stott, p. 23.

Origin of name. The specific name *fascicostatus* reflects the predominantly fasciculate bundling habit of the last preserved whorl of the holotype.

Type specimen. GSC Cat. 17247 reproduced in Pl. 35, fig. 2; Pl. 39, fig. 2; Figure 55a is designated herewith as the holotype.

Material. One specimen, GSC Cat. 17247 from GSC loc. 37867 and one specimen, GSC Cat. 77134 from GSC loc. 24024.

Locus typicus. Ellef Ringnes Island, Sverdrup Archipelago, N.W.T. GSC loc. 37867 situated about 3 km east of Isachsen Weather Station on the north bank of the delta of a nameless creek slightly less than 0.8 km from its mouth and less than 15 m above sea level.

Stratum typicum. Upper part of the Deer Bay Formation. Some part of its *Siberiptychites*-bearing beds. The concretionary bed that has yielded *S.* (*S.*) *fascicostatus* sp. nov. is probably situated 61 to 76 m lower stratigraphically than the beds of GSC loc. 21899 containing *Ringnesiceras tozeri* Kemper and Jeletzky provided that the beds between these two localities are as horizontal as they appear to be (W.W. Heywood, personal communication in 1963).

Diagnosis. A *Siberiptychites* (*Siberiptychites*) species characterized by early to intermediate whorls that are about as high as they are wide and an early adult? external suture line with four auxiliary lobes. Two lateral lobes and the first and second auxiliary lobes are situated on the flank. The last known intermediate whorl develops a predominantly fasciculate bundling habit.

Measurements in mm

Specimen	Shell diameter	Umbilicus (percent)	Whorl's height	Whorl's width	Ratio height/width
GSC Cat. 17247	64 (at oral end)	14.5 (23)	30	30.5	1.0 (appr.)
GSC Cat. 77134	35 (est)	8.5 (24)	20.5	18	1.14 (appr.)
GSC Cat. 77134	52 (est.) (at oral end)	11.5 (22)	25.5	25.5 (appr.)	1.0 (appr.)

Description

Whorl shape and proportions. Two earliest known, intermediate whorls are represented by the specimen GSC Cat. 77134 (Pl. 61, fig. 1). The earliest part of the inner whorl (probably either the fourth or the fifth from the protoconch) appears to be undeformed (see the table for its measurements). The whorl is uniquely slender for the genus and subgenus *Siberiptychites*, its height being either subequal to or even somewhat greater than its width. The adapical cross-section is an approximately egg-shaped oval (Pl. 61, fig. 1B), with the maximum width situated approximately one-third of the way upflank. The following two thirds of the flank is only slightly convex and contracts slightly but increasingly upflank until it merges into the illdelimited, approximately regularly arched venter.

Addorsally from the level of maximum width the adapical cross-section contracts slightly but increasingly fast to the broadly and regularly rounded umbilical shoulder which grades into more broadly rounded and less convex, low umbilical wall forming an angle of some 45 to 50 degrees with the plane of symmetry.

The next three-quarters of the whorl are slightly to strongly deformed and more or less weathered for the most part. However, the flanks appear to be approximately flat and subparallel oriented in the middle of this interval (Pl. 61, fig. 1B) and to be better delimited from the somewhat more narrowly rounded ventral shoulder and the regularly arched venter than before. The maximum width of the whorl appears now to be situated just above the umbilical shoulder.

The apparently undeformed oral cross-section of this whorl (Pl. 61, fig. 1B) has the height of about 52 mm (see the table for other measurements). This cross-section is distinctly less slender than the last and has a more narrow umbilicus. The maximum width of this distinctly egg-shaped cross-section is situated at the abrupt but narrowly rounded umbilical shoulder. The umbilical wall is only slightly convex and moderately high, it forms an angle of 70° to 75° with the plane of symmetry. The umbilicus is step-like shaped. The flanks are but slightly convex. They converge distinctly and almost evenly (at angles of 10 to 15 degrees) to the barely perceptible, very broadly rounded ventral shoulder where the contraction increases somewhat. The venter is somewhat narrowly rounded.

Both whorls are moderately involute with about five-sixths of preceeding whorls covered by the succeeding whorls (Pl. 61, figs. 1A, 1C).

The larger specimen GSC Cat. 17247 (Pl. 35, fig. 2; Pl. 39, fig. 2) with a maximum preserved shell diameter of about 64 mm (see table of measurements for its other dimensions) presents older, intermediate growth stages. It is completely septate, which precludes any definitive conclusions concerning the adult size of our form. Its cross-section, which is shaped and proportioned like the oral cross-section of the smaller specimen, is somewhat laterally deformed on the right side (see Pl. 35, fig. 2B). The cross-section is rounded-trapezoidal with the maximum width situated at the level of the umbilical shoulder. The only slightly convex flanks contract slightly and more or less evenly all the way to the broadly rounded and ill-defined ventral shoulder. The contraction increases strongly on the shoulder and the venter resulting in an obtuse arching and a distinct flattening of the latter.

A narrowly rounded umbilical shoulder separates the flanks from only gently inclined (75 to 80 degrees with the plane of symmetry; see Pl. 35, fig. 2A), slightly convex umbilical wall. Though about 85 per cent of the preceding whorls are concealed, the shallow, moderately involute (about 22 per cent) umbilicus has a distinctly step-like appearance.

Sculpture. The early whorls are largely concealed by later ones so that only their inner margins are visible in the two available examples (e.g. GSC Cat. 17247 and 77134). They bear delicate and closely spaced, sharp-topped primary ribs (Pl. 35, fig. 2A; Pl. 61, fig. 2C). These begin in the middle of the umbilical wall where they are backwardly inclined at 55-65 degrees. They gradually become stronger and more elevated closer to and on the umbilical shoulder while starting to bend forward. This results in a distinctly forwardly convex (comma-like) shape. There are 29-30 primaries on the last concealed whorl (estimated shell diameter 30 mm). The presence of two or three exceptionally wide interspaces suggests the occurrence of constrictions. The shell-covered primaries are considerably higher and more sharp-topped than their internal casts.

From about 34 mm shell diameter (estim.) the whole whorl is exposed in GSC 77134 (Pl. 61, figs. 1A-1C), so that the secondary ribs become visible. By this stage the primaries appear not to differ from those of the concealed whorls. They bifurcate at about the middle of the flank. For about a quarter of a whorl no further branching occurs, resulting in simple dichotomous bundles, of which a maximum of 8 are visible. However, one or two single intercalated secondaries, restricted to the middle and upper flank, occur between the bundles. Then trivirgatitpartitous rib bundles appear (Pl. 61, fig. 1C), heralding the end of the simple dichotomous sculptural stage. They result of a repeated bifurcation of their posterior secondary. The primaries of this predominantly trivirgatitpartitous sculptural stage are distinctly higher, more heavily built, though non-bullate, and distinctly shorter; they extend only across the lower third of the flank before bifurcating. What appears to be a single rib attached to its own primary occurs between some trivirgatitpartitous bundles. This predominantly trivirgatitpartitous stage lasts from about 36 mm shell diameter to the oral end in GSC Cat. 77134 and to about 51 mm on the apical third of the last preserved whorl of GSC Cat. 17247.

In the earliest growth stage visible (GSC Cat. 77134; Pl. 61, fig. 1C) there are some 28-29 primary ribs per whorl. In the most advanced growth stage visible (the last preserved whorl of GSC Cat. 17247) the number reduces to 24 as they become increasingly stronger and more widely spaced towards the oral end (Pl. 35, fig. 2A). The last few primaries are slightly bullate.

On the final two-thirds of the whorl of GSC Cat. 17247 (Pl. 35, fig. 2A, B) the primaries branch on the lowermost one-third to one quarter of the flank to form quadrifasciculate to trifasciculate bundles. Only a few trivirgatitpartitous bundles are intercalated with them. This bundling habit is typical of the predominantly fasciculate variant of the predominantly quadripartitous sculptural stage of *Siberiptychites* (see p. 138, 139 for further details). Unlike in earlier sculptural stages, where all the supplementary ribs are attached firmly to their relatively longer primaries, one or more of the supplementary ribs of this stage is only indistinctly attached. Furthermore, some single ribs devoid of their own primaries are intercalated between some of the indistinctly formed bundles. Only the early part of this stage is preserved in *S.* (*S.*) *fascicostatus*.

From when they first become visible the supplementary ribs are inclined forward, gently on the flank but more strongly towards the venter. This results in a distinctly flexuous, forwardly concave appearance. They bend forward over the venter (Pls. 37, fig. 2B and 61, fig. 1B), where they are neither weakened nor interrupted. The forward bend is considerably reduced on the last two-thirds of the oralmost preserved whorl. Here the supplementary ribs become considerably lower and more or less round-topped in both shell-covered and internal mould preservations. Furthermore, they are distinctly more delicate and more closely spaced than before, and therefore contrast all the more markedly with their increasingly stronger and more widely spaced primaries (Pl. 35, figs. 2A, 2B).

There are 90 or 91 supplementary ribs on the last preserved whorl, with a resulting bundling coefficient of only 3.8. Only one ill-defined, shallow constriction was observed on the first third of the last preserved whorl of GSC Cat. 17247.

Suture line. Complete external, presumably early adult suture line was only observed on the last whorl of GSC Cat. 17247 (Pl. 35, fig. 2A; Figure 55a). It differs from all other adult external sutures of *Siberiptychites* in the presence of four auxiliary lobes and in the positioning of the first and second auxiliary lobes on the whorl's flank. The third and fourth auxiliaries are situated respectively within the outer third and in the middle of the umbilical wall. A tiny, tack-like element, interpreted herein as a lobule, is visible just at the umbilical seam.

The first lateral lobe is either slightly shorter than or about as long as the ventral lobe. The two are subequally wide and similarly complexly denticulated. The first lateral is relatively sturdy (length/width ratio only 2.8), parallel-sided, and asymmetrically trifid; it is disproportionally large and much more complexly denticulated than the other lobes.

The moderately deeply denticulated first lateral saddle is somewhat wider than the ventral and the first lateral lobes (Pl. 35, fig. 2A, Figure 55a).

The markedly asymmetrically trifid and only shallowly denticulated second lateral lobe is only half as long and one-third as wide as the first lateral lobe.

The but slightly denticulated second lateral saddle is only as wide as the first lateral saddle.

The length and width of the parallel-sided, irregularly trifid and shallowly denticulated first auxiliary lobe comprise less than one-third of those of the second lateral lobe.

The narrow and only slightly denticulated fourth lateral saddle is about one and a half times wider than the first auxiliary lobe.

The second auxiliary lobe, which is situated on the innermost flank, is similar to the first auxiliary, except in being slightly smaller.

The only slightly denticulated fifth lateral saddle, which extends from the innermost flank to the outer quarter of the umbilical wall, is exceptionally wide (twice as wide as the fourth saddle).

The length of the spicular, almost symmetrically trifid and only slightly notched third auxiliary lobe is about three-quarters that of the second auxiliary.

The only slightly denticulated sixth lateral saddle is as narrow proportionally as is the fourth saddle.

The fourth auxiliary lobe is shaped and denticulated like the third auxiliary but its length is only about two-thirds that of it. Finally, the exposed outer part of the seventh lateral saddle is somewhat wider than the whole of the sixth saddle.

The lateral part of the suture line is approximately straight and ascendant at 10 to 15 degrees. Then it bends over the second auxiliary lobe, becomes subradial to slightly ascendant and maintains this course to the umbilical seam.

The adjacent sutures are separated by considerable distances which confirms their early adult character.

The poorly and incompletely exposed external sutures of GSC Cat. 77134 are similar to those of GSC Cat. 17247 in all observable details.

Affinities and differences. *Siberiptychites* (*Siberiptychites*) *fascicostatus* is assigned to the subgenus *Siberiptychites* because of the presence of rare and illdefined constrictions combined with the presence of a characteristically narrow umbilicus, typically numerous and crowded primary ribs and a characteristic sequence of sculptural stages. Its presumably early adult external suture line is also typical of the subgenus, except for the presence of the fourth auxiliary lobe and the positioning of the second auxiliary lobe on the adumbilical part of the flank. These two distinctions, and the uniquely slender whorl proportions, do not justify even the subgeneric separation of *S.* (*S.*) *fascicostatus* from the rest of *Siberiptychites* s. str. species in view of its otherwise typical morphology. The positioning of auxiliary lobes is known to vary strongly within *Siberiptychites* s. str. (see in the subgeneric description for further details).

Within the subgenus *Siberiptychites*, *S.* (*S.*) *fascicostatus* resembles most closely *S.* (*S.*) n. sp. aff. *stubendorffi*, with which it shares the presence of a distinctly *Astieriptychites*-like, mostly fasciculate bundling habit of advanced whorls. It differs in a much more slender and differently shaped whorl section at equivalent growth stages, the positioning of the second auxiliary lobe on the adumbilical part of the flank, and the presence of the fourth auxiliary lobe. The second auxiliary of *S.* (*S.*) n. sp. aff. *stubendorffi* is situated instead either on the umbilical shoulder or on the outer part of the umbilical wall. These distinctions are judged to be sufficient for the full specific differentiation of these two forms, in spite of a rather unsatisfactory state of knowledge of their morphology, ranges of infraspecific variation, and time ranges.

From *S.* (*S.*) *stubendorffi* the species differs in its much more slender and differently shaped whorl section at equivalent growth stages and the presence of four auxiliary lobes in its early adult external suture lines. Furthermore, the first and second auxiliary lobes of *S.* (*S.*) *fascicostatus* are situated on the whorl's flank. Finally, it has a predominantly fasciculate, *Astieriptychites*-like sculpture on those intermediate whorls which bear bidichotomous to variegated variants of predominantly quadripartitous sculpture in the other species. These distinctions justify full specific differentiation of *S.* (*S.*) *fascicostatus* from the other species, in spite of the fact that their more advanced and adult growth stages cannot be compared.

Because of its egg-shaped to rounded-trapezoidal, similarly slender whorl cross-section, *S.* (*S.*) *fascicostatus* resembles *Bodylevskites* Klimova 1978. However, this similarity is obviously homoeomorphic in character because of the very different morphology of their suture lines.

Among morphologically similar North Siberian polyptychitinids, the rather peculiar "*Tollia* (*Polyptychites*?)" *mira* Voronets (1962, p. 69, 70; Pl. XLI, figs. 3a, 3b; Figure 26) resembles the holotype of *S.* (*S.*) *fascicostatus* closely where the shape and proportions of its only exposed whorl are concerned. However, its somewhat obscurely described and figured bundling habit appears to be dominated by bidichotomous instead of either trivirgatitpartitous or fasciculate bundles and it has no less than 108 supplementary (i.e secondary plus tertiary) ribs against 91 to 92 in our specimen. Furthermore, its generally closely similar external suture line has only three auxiliary lobes at a comparable whorl diameter. However, the two forms appear to be closely allied because of the recorded presence of four constrictions on the last preserved whorl of the only known representative of "*Tollia* (*Polyptychites*?)" *mira* combined with its slender, *S.* (*S.*) *fascicostatus*-like whorl cross-section.

The shape, proportions and sculpture of the exposed two whorls of GSC Cat. 77134 are indistinguishable from those of the comparably large holotypes of "*Polyptychites*" *densicosta* Pavlow and "*Polyptychites*" *conferticosta* Pavlow (1914, p. 26, 27; Pl. V, fig. 3, 4). The same is true of the early third of the last preserved whorl of the holotype of *S.* (*S.*) *fascicostatus*, which is slightly larger than "*P.*" *densicosta* and considerably larger than "*P.*" *conferticosta*. The exposed and concealed whorls of GSC Cat. 77134 have, in particular the same number of primary ribs as the holotype of "*P.*" *conferticosta*. However, the external suture line of the latter species remains unknown while that of the holotype of "*P.*" *densicosta* is all but invisible (and consequently indeciferable) and quite inadequately described (no data are provided about the number of its auxiliaries!). Furthermore, neither of these two North Siberian forms exhibits constrictions and their presence is not mentioned in their descriptions. Therefore, "*P.*" *densicosta* and "*P.*" *conferticosta*, as defined by their unique, poorly preserved holotypes, cannot be assigned to the subgenus *Siberiptychites* and are tentatively considered herein as only homoeomorphically similar, true representatives of *Polyptychites* either allied to or conspecific with *P. ramulicosta* Pavlow.

The considerably larger (terminal shell diameter about 77 mm) North Siberian polyptychitinid described and figured as *Polyptychites conferticosta* Pavlow 1914 by Voronets (1962, p. 76; Pl. XLVII, figs. 2a, 2b) agrees closely with the holotype of *S.* (*S.*) *fascicostatus* in the shape and proportions of its whorl. However, unlike the Canadian specimen, the trivirgatitpartitous bundling habit persists right to its oral end. Furthermore, this North Siberian specimen is considerably more sparcely and coarsely ribbed on the oral half of its last preserved whorl. The character of the external suture line of this specimen is unknown and the constrictions are neither visible in its photographs nor mentioned in its description. Therefore, it is believed to represent the more advanced growth stages of the same species of true *Polyptychites* as the holotype of "*P.*" *conferticosta*. At any rate there is no valid reason either to transfer it to the subgenus *Siberiptychites* or to synonymise it with *S.* (*S.*) *fascicostatus*.

Stratigraphic relationships and age. The holotype of *S.* (*S.*) *fascicostatus* was found on Ellef Ringnes Island at the previously described GSC loc. 37867 (see p. 151 for further details), associated with *S.* (*S.*) *stubendorffi*, *S.* (*P.*) *middendorffi* var. *incrassata* and *Buchia sublaevis* (Keyserling). Hence this locality is correlative with the *Siberiptychites* (*Siberiptychites*) *stubendorffi*-bearing beds 16 and 17 of the measured section of the Deer Bay Formation on Amund Ringnes Island. The stratigraphic position of this fossil locality in relation to the overlying Deer Bay/Isachsen contact was not determined but is believed to be in order of 91.5 to 106.5 m.

The smaller specimen GSC Cat. 77134 was also found on Ellef Ringnes Island, N.W.T. Its fossil locality GSC 24024 is situated (according to the label) about: "3 miles north of Salt Dome (the Dumbbell Salt Dome must be meant; writers' remark)". No data are available about the formational origin of this specimen, which must be derived from the upper Deer Bay Formation.

Subgenus *Pseudoeuryptychites* Jeletzky 1986

Type species. *Euryptychites pavlovi* Voronets 1962.

Derivation of name. To stress the superficial morphological similarity of the subgenus to the homoeomorph *Euryptychites* Pavlow 1914.

Diagnosis. Large (terminal adult shell diameter 200 mm or ?more), *Siberiptychites*-like ammonites distinguished by the presence of the initial globular growth stage and the *Euryptychites*-like shape and proportions of all growth stages with the shell diameter exceeding 45 to 50 mm. The sculpture is at first largely (on the flanks) and then completely (except for the umbilical bullae) lost on the adult penultimate and, apparently, adult ultimate whorls. The juvenile external suture line is *Siberiptychites* s. str.-like but the adult suture differs in a much greater complexity and the positioning of all three auxiliary lobes on the umbilical wall. All of these auxiliaries are relatively much larger, more slender, and more deeply denticulated than their counterparts in *Siberiptychites* s. str., true *Euryptychites*, and *Hollwediceras*. Otherwise, *Pseudoeuryptychites* differs from the true *Euryptychites* and *Hollwediceras* in the same way as *Siberiptychites* s. str. does.

Type area. Central part of Northern Siberia (Anabar-Khatanga basin).

Stratigraphy and age. Lower Valanginian. Regional *Temnoptychites syzranicus* and *Polyptychites michalskii* zones, with the exception of the lower part of *Temnoptychites syzranicus* Zone where *Bodylevskites* is associated with *Siberiptychites stubendorffi* (Klimova, 1978, p. 53; 1981, p. 74; Gol'bert et al., 1981, p. 56, 57, Tables 3, 4). Equivalents of the middle part of *Polyptychites michalskii* Zone in the Sverdrup Basin. See the descriptions of *Pseudoeuryptychites pavlovi*, *P. middendorffi* and *Pseudoeuryptychites* n. sp. indet. A and Figure 62 for further details.

Geographical range. Northern Siberia, Arctic Canada (Sverdrup Basin), and Spitsbergen. Probably present elsewhere in high Boreal basins of the Eurasian Arctic and North America also.

Discussion. Kemper and Jeletzky (in Kemper, 1977, p. 3) have noted that the subgenus *Siberiptychites* included *Cadoceras*-like forms resembling *Euryptychites* Pavlow 1914 but possessing features diagnostic of *S. stubendorffi*, such as the constrictions and the third auxiliary lobe in the adult external suture line. A subsequent, more detailed study of these *Cadoceras*-like *Siberiptychites* (Jeletzky, 1986) revealed that they are a well defined, morphologically distinctive evolutionary offshoot of its main lineage (i.e. *Siberiptychites* ex gr. *stubendorffi*). Furthermore, all of the North Siberian and European Arctic *Cadoceras*-like polyptychitinids assigned to the European genus *Euryptychites* by Pavlow (1914, p. 36-38, Pl. XI, figs. 1-3) and subsequent Russian workers (e.g. Voronets, 1962, p. 78-82, Pl. XXXIX, fig. 2; Pl. XL, fig. 2a, b; Pl. XLIX, fig. 1a, b; Pl. XLII, fig. 1; Pl. L, fig. 2; Pl. XLVIII, fig. 1; Pl. LI, fig. 1a, b; Pl. LII, fig. 1; Figures 29-31; Bodylevsky, 1968, p. 313; Pl. 72, fig. 1a, b; and Yershova, 1980, Pl. IV, fig. 2) were found to belong to that offshoot. Jeletzky (1986, p. 352-354) erected a new subgenus *Pseudoeuryptychites* for these *Cadoceras*-like *Siberiptychites*, explored their biochronology and geographical distribution, and described their Canadian representatives. Further research of *Pseudoeuryptychites* carried out during the preparation of this paper has revealed its additional important distinctions from *Siberiptychites* ex gr. *stubendorffi* which necessitated a reapprisal of its scope. *Pseudoeuryptychites* is now interpreted as a divergent offshoot of *Siberiptychites* s. str. which includes "*Siberiptychites*" *middendorffi* as its most primitive form.

The purely homoeomorphic nature of the morphological similarity of *Euryptychites* s.s. (as defined by its type species *E. latissimus* (Neumayr and Uhlig, 1881)) with the North Siberian cadicone polyptychitinids assigned to that genus by Pavlow (1914, p. 36) and other Russian workers, is revealed first of all by an entirely different ontogenetic development of their sculpture and whorl shape. As indicated earlier in the description of

Siberiptychites and below in the description of *S.* (*Pseudoeuryptychites*) *middendorffi* and *S.* (*P.*) *pavlovi*, this ontogeny resembles closely that of *Siberiptychites* s.s. Furthermore, all these cadicones possess numerous *Siberiptychites* s.s.-like constrictions completely absent in true *Euryptychites*. The adult external sutures of these two taxa also differ markedly. Unlike the sutures of *S.* (*P.*) *pavlovi* and other *Pseudoeuryptychites* species (Figures 56a, 56b, 57a-57c, 58a), those of *E. latissimus* (Neumayr and Uhlig, 1881, p. 158, Pl. XXVIII, fig. 1b; this paper, Fig. 14a-14c) and other *Euryptychites* species have, as a rule, only two auxiliary lobes. These auxiliaries are relatively smaller and simpler structures separated from each other and from the second lateral lobe by relatively wider saddles. Most *Euryptychites* sutures also differ in the stubby, downward-tapering appearance of their lobes.

The resemblance of *Pseudoeuryptychites* to the late early to earliest late Valanginian Central European *Hollwediceras* gen. nov. is also a matter of homoeomorphy only. The European representatives of this genus do exhibit a similarly late development of the *Euryptychites*-like shape and proportions of the whorl. However, they always lack the constrictions that are so characteristic of *Pseudoeuryptychites*. Furthermore, *Hollwediceras* ex gr. *sphaericus-praelatus* are characterized by a different bundling habit of intermediate whorls, dominated by polyptychous to tridichotomous bundles (e.g. Koenen, 1902, Pl. IV, figs. 1, 2; Pl. LV, fig. 1; this paper, p. 87). The equivalent whorls of all *Pseudoeuryptychites* forms exhibit instead either a trivirgatitpartitous (see Figure 9) or a predominantly quadripartitious bundling habit, which is similar to that of the equivalent and younger whorls of *Siberiptychites* s.s. Finally, all better known representatives of *Pseudoeuryptychites* (e.g. *S.* (*P.*) *pavlovi*, *S.* (*P.*) *middendorffi* and *S.* (*P.*) *splendens*; see Pavlow, 1914, Pl. XI, fig. 3; Voronets, 1962, Pl. LXII, fig. 1; Bodylevsky, 1968, Pl. 72, fig. 1 and the specific descriptions below) exhibit a *Siberiptychites* s.s.-like sequence of various whorl shapes and sculptural stages that are not present in *Hollwediceras* ex gr. *sphaericus-praelatus*. This sequence of whorl shapes and sculptural stages is described here in the generic description of *Siberiptychites* (p. 134-136).

The adult external suture line of *Hollwediceras* ex gr. *sphaericus-praelatus* may have either two or three auxiliary lobes (e.g. Koenen, 1902, Pl. IV, figs. 1, 2, 3, 5; Pl. LV, figs. 1, 2; this paper, Figures 34a, 34b). The variant with three auxiliaries resembles closely the adult suture of *Pseudoeuryptychites* (Figures 56a, 56b, 57a-57c, 58a), except in the positioning of the auxiliaries and the ontogenetic-phylogenetic development. The adult, six-lobed external suture of *Hollwediceras* ex gr. *sphaericus-praelatus* develops out of the five-lobed late juvenile suture *via* the addition of the third auxiliary at the umbilical seam and the concurrent displacement of the first auxiliary onto the adumbilicalmost part of the flank. Furthermore, the six-lobed suture of this species group can be traced back phylogenetically to the adult external suture of ancestral *Polyptychites* ex gr. *pavlowi* that always possesses only two auxiliary lobes (p. 44, 50; Figure 19). The external suture of *Pseudoeuryptychites*, in contrast, has three auxiliary lobes in the earliest growth stages known (Figures 55b, 58a and in the descriptions of *Siberiptychites* (*Pseudoeuryptychites*) *middendorffi* and *S.* (*P.*) n. sp. indet. A). This late juvenile suture has only two auxiliaries on the umbilical wall and is *Siberiptychites* (*Siberiptychites*)-like in this and other respects. The adult *Pseudoeuryptychites* suture develops out of this juvenile suture *via* the adumbilical displacement of the first auxiliary onto the outermost part of the umbilical wall (Fig. 57a, 58a). Furthermore, the adult *Pseudoeuryptychites* suture can be traced phylogenetically into the much less denticulated adult external suture of *S.* (*S.*) *stubendorffi* (Pavlow, 1914, Pl. VI, fig. 1c; Klimova, 1981, Figure 3b; this paper, Figures 52b, 52c, 53a, 53b), which also has three auxiliary lobes. However, only two auxiliaries of this suture are situated on the umbilical wall. The inferred palingenetic evolutionary development of the *Siberiptychites* external suture features a gradual displacement of the first auxiliary lobe onto the outer part of the umbilical wall and a concurrent crowding of all three auxiliaries there combined with a gradual increase in the complexity of the adult suture. This ontogenetic and phylogenetic development is quite unlike the above discussed, well documented, ontophylogenetic development of the external suture of *Hollwediceras* ex gr. *sphaericus-praelatus*.

Pseudoeuryptychites differs from *Siberiptychites* s. str. first of all in the above discussed distinctive character of its adult external suture line, which is characterized by the positioning of all three auxiliary lobes on the umbilical wall, combined with a much greater complexity, depth of denticulation, and size of all its elements. This characteristic adult suture is now known in *S.* (*P.*) *middendorffi*, *S.* (*P.*) *pavlovi*, and *S.* (*P.*) n. sp. indet. A while being absent in all better known *Siberiptychites* s. str. forms.

The second important distinction is the entirely *Euryptychites*-like shape and proportions of all advanced and adult whorls of *Pseudoeuryptychites* beginning with the shell diameter of 45-50 mm. This second *Euryptychites*-like growth stage (p. 135, 136), which is absent in *Siberiptychites* s., str., except for the sturdy variant of *S.* (*S.*) *stubendorffi*, mostly has an acute umbilical shoulder (Pavlow, 1914, Pl. XI, figs. 1, 2a-c, 3; Voronets, 1962, Pl. XLII, fig. 1; Pl. XLVII, fig. 1; Pl. L, fig. 2; Pl. LI, fig. 1a, b; Pl. LII, fig. 1; this paper, Pl. 38, fig. 2B; Pl. 67, fig. 2B; Figure 54f). However, the umbilical shoulder remains narrowly rounded throughout this stage in the otherwise typical *Siberiptychites* (*Pseudoeuryptychites*) *middendorffi* which was previously assigned to the subgenus *Siberiptychites* s. str. because of this feature (Jeletzky, 1986, p. 354).

The third important distinction is a much larger shell size of adult *Pseudoeuryptychites* estimated to be about 200 mm or ?more. There are no known exceptions to this rule. All suitably preserved representatives of *Siberiptychites* s. str. are, in contrast, estimated to have adult shell sizes ranging from 120 to 140 mm.

The fourth important distinction is the prevalent to almost complete (except for the umbilical bullae and constrictions) loss of the ornament on the adult penultimate and/or adult ultimate whorls of all *Pseudoeuryptychites*, including *S.* (*P.*) *middendorffi*. The early part of the adult ultimate whorl of all suitably preserved representatives of *Siberiptychites* s. str. remains distinctly (albeit less markedly) sculptured, with the marked weakening of ribbing restricted to the mid-flank. The same is inferred to be true of the still unknown oral part of its adult ultimate whorl.

Finally, the fifth and last distinction appears to be the presence of the initial globular growth stage in *S.* (*P.*) *middendorffi* (see p. 134, 135) which is the most primitive representative of *Pseudoeuryptychites*. This feature is absent in *S.* (*S.*) *stubendorffi* where the next older first *Euryptychites*-like growth stage begins at the protoconch and persists through the earliest three whorls (Klimova, 1981, p. 75, Figures 2-1 to 2-3 and p. 134, 135 of this paper). Though this initial globular growth stage is not known in other representatives of *Pseudoeuryptychites*, it is believed to be a prophetic (or proterogenetic) feature that arose in *S.* (*P.*) *middendorffi* and persisted in all other, more advanced *Pseudoeuryptychites* forms.

In spite of the above distinctions, *Siberiptychites* s. str. and *Pseudoeuryptychites* must be closely related; they both exhibit frequent constrictions throughout the ontogeny and their ontogenetic sequences of sculptural stages and shell shapes closely resemble each other (p. 134-139). These two taxa coexisted in the same high Boreal basins in approximately contemporary lower Valanginian beds without any intergradation, except near the base of their time ranges (i.e. via the earliest representatives of *S.* (*P.*) *middendorffi*). This indicates that they are independent lineages that arose out of the same rootstock (i.e. the earliest known forms of *S.* (*S.*) ex gr. *stubendorffi*). The most primitive representative of *Pseudoeuryptychites* — *S.* (*P.*) *middendorffi* — appears to be a connecting link between the typical representatives of *Pseudoeuryptychites* and these earliest *Siberiptychites* s. str. The recorded detailed stratigraphic relationships of these forms (see their specific descriptions for further details) support this conclusion. *Pseudoeuryptychites* appears to be a short-lived offshoot of the main *Siberiptychites* s. str. stem that died out without issue (Figure 11). Therefore, it is assigned a subgeneric rank only.

The pronounced distinctions of the adult external suture line of *Pseudoeuryptychites* from its early and late juvenile sutures (*see* p. 168-171 and 161) suggest that their modification is a late addition (an anaboly in terms of Severtsov's, 1939, p. 483-499 evolutionary terminology) to the sutural ontogeny reflecting the recapitulatory mode of evolution. This farreaching complication of the adult suture and the relative increase of the size of all its lobes in comparison with the ancestral *S.* (*S.*) ex gr. *stubendorffi* appear to be connected with a major relative increase of the adult size of *Pseudoeuryptychites*; these new features have probably evolved because of the need to assure a more secure attachment of the relatively enlarged adult soft body of this subgenus to its shell.

Siberiptychites (*Pseudoeuryptychites*) *middendorffi* (Pavlow, 1914)

Plate 32, fig. 4; Plate 34, figs. 2, 3; Pl. 36, fig. 2;
Pl. 39, fig. 3,
Figures 54d, 55b, 55c; 56a, 56b

Synonymy

1914	*Polyptychites middendorffi* Pavlow, p. 31-33, Pl. VII, fig. 1, 2.
1914	*Polyptychites middendorffi* var. *incrassata* Pavlow, p. 32, Pl. VI, fig. 2.
1964	*Polyptychites stubendorffi* var. *middendorffi* Jeletzky, p. 48, Pl. X, fig. 5 (non fig. 2).
1965b	*Polyptychites* (*Euryptychites*) *stubendorffi* var. *middendorffi* Jeletzky, p. 11, 12, Fig. 1f.
1977	*Polyptychites stubendorffi* Kemper, p. 3, Figure 3, in part (the specimens GSC Cat. 77102 and 77100 from the Bed 16 only).
1986	*Siberiptychites* (*Siberiptychites*) *middendorffi* Jeletzky, p. 354.

Type specimen. The large original of Pavlow's (1914) cotype of "*Polyptychites*" *middendorffi* reproduced in his Plate VII, fig. 1 is selected herewith as lectotype. The juvenile cotype reproduced in Plate VII, fig. 2 is judged to be unsuitable as a type specimen. The third specimen assigned by Pavlow (1914, Pl. VI, fig. 2) to "*P.*" *middendorffi* is unavailable for selection. It was originally designated as "*P.*" *middendorffi* var. *incrassata* and so is a nomenclatorially valid taxon in its own right.

Material. Four specimens from the GSC localities 37869, C-4749, and 91310.

Diagnosis. A *Pseudoeuryptychites* species characterized by the persistence of a narrowly rounded (instead of acute) umbilical shoulder through the entire known extent of its second *Euryptychites*-like growth stage, including the adult penultimate whorl. The umbilicus is uniquely narrow (21-25 per cent) and *Siberiptychites* s. str.-like.

Measurements in mm

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
GSC Cat. 77102	142	36(25%)	59(42%)	45(33%)	—	7,0
GSC Cat. 77100	42	9(21%)	19(45%)	14(34%)	21	21

Description

Historical and general remarks. So far as the writers know, no additional representatives of *S.* (*P.*) *middendorffi* (Pavlow, 1914) have been described and figured in the Eurasian literature since its erection by Pavlow (1914, p. 31-33, Pl. VI, fig. 2; Pl. VII, fig. 1, 2). As already mentioned, the East Greenland specimen described and figured as *Polyptychites* cf. *middendorffi* by Donovan (1953, p. 102, 103, Pl. 21, fig. 2) is actually a sturdy representative of *S.* (*P.*) *stubendorffi*.

In North America *S.* (*P.*) *middendorffi* (Pavlow) was unknown until Jeletzky (1964, p. 48, Pl. X, figs. 2, 5) figured and briefly described it from the Valanginian rocks of the Sverdrup Basin. However, only the specimen figured in Pl. X, fig. 5 as *Polyptychites stubendorffi* (Schmidt) var. *middendorffi* (Pavlow) actually belongs to *S.* (*P.*) *middendorffi* var. *incrassata* Pavlow. The other specimen reproduced in Pl. X, fig. 2 is a sturdy representative of *S.* (*P.*) *stubendorffi*. Additional material of *S.* (*P.*) *middendorffi* was later collected in the Sverdrup Basin by the Geological Survey geologists and Kemper (1977, p. 3, Figure 3). However, it was originally identified as *S.* (*S.*) *stubendorffi* and is described and figured as *S.* (*P.*) *middendorffi* for the first time in this paper. *S.* (*P.*) *middendorffi* was assigned to the subgenus *Sibe*riptychites by Jeletzky (1986, p. 354) but is here transferred to the subgenus *Pseudoeuryptychites* for reasons explained in its subgeneric description on p. 161, 162.

In spite of the absence of modern descriptions and figures, *S.* (*P.*) *middendorffi* (Pavlow) appears to be a common species in the so called middle Valanginian (recte upper lower Valanginian) of Northern Siberia as it is repeatedly cited from the *Polyptychites michalskii* Zone of that region (e.g. Saks et al., 1963, p. 178, 183; Gol'bert et al., 1981, p. 59, Table 4).

The material of *S.* (*P.*) *middendorffi* (Pavlow) and its var. *incrassata* (Pavlow) available to all workers beginning with Pavlow (1914) and including the writers, is scarce and represented by incomplete shells. The present study is based on only four definitively identifiable Canadian specimens, which include juvenile, intermediate and advanced growth stages of the species, and a re-evaluation of its Siberian material. Fortunately, the three small to medium-sized phragmocones permit for the first time a study of most of the sculptural growth stages of the species and of the ontogenetic development of its external suture line. In combination with the type material of *S.* (*P.*) *middendorffi* described and figured by Pavlow (1914, p. 31-33, Pl. VI, fig. 2; Pl. VII, fig. 1, 2), they provide a reasonably complete picture of the morphology and ontogenetic development of the species.

Whorl shape and proportions. The earliest growth stage has an equidimensional, approximately globular shape and appears to lack completely the umbilical and ventral shoulders. The umbilicus is involute. This **globular growth stage** (see p. 134, 135 for further details) was observed in the specimens GSC Cat. 77100 (Pl. 32, fig. 4; Pl. 34, fig. 3E; Figure 52d) and 77099 (Pl. 40, fig. 2B) belonging to the typical variant and in the specimen GSC Cat. 17251 (Pl. 40, figs. 3A-3F) belonging to *S.* (*P.*) *m.* var. *incrassata*. It is estimated to extend over the earliest one to ?two whorls (i.e. to the shell diameter of about 3.5 to ?4 mm in the first two specimens. However, it appears to last through the earliest three or ?four whorls (i.e. to the shell diameter of 5 to ?6 mm) in the third specimen belonging to var. *incrassata*.

The next growth stage has a much wider than high, crescent-like, expressly *Euryptychites*- and *Pseudoeuryptychites*-like (except for the narrowly rounded umbilical shoulder) whorl cross-section and a moderately involute, funnel- to step-like umbilicus. It was observed in GSC Cat. 77100 (Pl. 32, fig. 4; Pl. 34, fig. 3E; Figure 54d) and, apparently, in the GSC Cat. 79099 (Pl. 40, fig. 2B) of the typical variant and in the GSC Cat. 17251 (Pl. 39, figs. 3F-3H) belonging to *S.* (*P.*) *m.* var. *incrassata*. This **first Euryptychites-like growth stage** (see p. 134, 135 for further details) appears to develop gradually but rapidly (over one-half whorl or so) out of the preceding globular growth stage and to last through one to one and a half whorls (approximately between the shell diameters of 3.5 to 9.5 mm) in the specimen GSC Cat. 77100 (Figure 54d) where it is best exposed. There, its earliest visible cross-section is about 4.2 mm wide and only 2.2 mm high (height/width ratio about 58 per cent) while its next and latest visible cross-section is about 4.5 mm wide and only 2.5 mm high (h/w ratio about 55 per cent). Their very broad and evenly but very low arched ventral rounding (i.e. flanks and venter combined) is markedly but not abruptly delimited from their much more narrow but approximately straight umbilical wall that forms an angle of 45 to 50 degrees with the shell's plane of symmetry. The fragment of the first *Euryptychites*-like growth stage preserved in GSC Cat. 17251 (Pl. 39, figs. 3F-3H) has a width of 10 mm and a height of only 5.8 mm (h/w ratio about 58 per cent) at the end and is estimated to represent a shell diameter of some 20 mm. Therefore, the first *Euryptychites*-like growth stage appears to extend to a considerably larger shell diameter in *S.* (*P.*) *m.* var. *incrassata* than it does in the typical variant. Unlike the GSC Cat. 77100, this cross-section is rounded-trapezoidal with the slightly convex, very broad venter distinctly delimited from the low, less convex flanks. The distinctly delimited umbilical shoulder is situated at the level of the greatest whorl width and the umbilical wall is convex. These distinctions appear to reflect a normal infraspecific variability.

The first *Euryptychites*-like cross-section merges rapidly into a considerably more slender, rounded-rectangular to hoof-like cross-section of the **Polyptychites rectangulatus-like growth stage** (see p. 135, 136). In *S.* (*P.*) *middendorffi* one can distinguish an early *Bodylevskites*-like phase of this stage resembling the sturdier late juvenile cross-section of that genus and a late *Polyptychites rectangulatus*-like phase resembling the more advanced cross-section of this form. GSC Cat. 77100 (Pl. 32, fig. 4; Pl. 34, fig. 3E; Figure 54d) offers the only good example of both phases. The early phase begins between the shell diameters of 11 and 15 mm and ends somewhat before the shell diameter of 22 mm where the whorl's width is about 10.5 mm and its height is about 9.5 mm (height/width ratio of about 90 per cent).

In GSC Cat. 77100 the early phase is replaced by a somewhat more sturdy (height/width ratio of 80 to 86 per cent), rounded-rectangular *Polyptychites rectangulatus*-like (compare Bogoslovsky, 1902, Pl. XVI, fig. 1b) late phase, in which the flanks are only slightly convex, subparallel, and separated by almost regularly rounded shoulders from the broad, feebly convex to low-arched venter and feebly convex umbilical wall. The maximum width of its whorls is situated at the umbilical shoulder and the umbilicus is deep, moderately involute (about 21 per cent) and step- rather than funnel-like. This late phase begins between the shell diameters of 22 and 29 mm in a cross-section with the whorl's width of 15 mm and its height of 12.4 mm (height/width ratio of 83 per cent); it persists through the next following two oralmost cross-sections with respective shell diameters of 39 mm (height/width ratio of 86 per cent) and 42 mm (height/width ratio of 80 per cent). The end of the entire *Polyptychites rectangulatus*-like stage is not reached in the last section but its exposed greater part must extend over some three whorls.

The clearly discernible *Polyptychites rectangulatus* growth stage of the considerably deformed specimen GSC Cat. 77099 (Pl. 40, fig. 2B) continues to at least the shell diameter of 53 mm before being replaced by the second *Euryptychites*-like growth stage. The former stage is also typically developed in the comparably large paratype of *S.* (*P.*) *middendorffi* (Pavlow, 1914, Pl. VII, fig. 2). It is not preserved in the GSC Cat. 17251 belonging to *S.* (*P.*) *m.* var. *incrassata* (Pl. 39, fig. 3) but an exceptionally early development of the second *Euryptychites*-like growth stage in this specimen (see below) suggests a considerable abbreviation of the *Polyptychites rectangulatus*-like growth stage comparative to the typical variant of the species.

The *Polyptychites rectangulatus*-like cross-section becomes, in its turn, rapidly replaced by the much wider and lower (height/width ratio 55 to 71 per cent) **second Euryptychites-like growth stage** (see p. 135, 136) which is similar to the first *Euryptychites*-like growth stage, except for a much larger size and much more advanced ontogenetic position. It begins within the last preserved one-quarter whorl of the GSC Cat. 77099 (Pl. 40, fig. 2A) where the last preserved cross section corresponds to the shell diameter of about 62 mm and has an entirely *Euryptychites*-like shape and proportions, except for the broadly rounded umbilical shoulder. Judging by Pavlow's (1914, p. 31, Pl. VII, figs. 1b, 1c) figures and measurements, the similar second *Euryptychites*-like growth stage begins at the same whorl diameter in the holotype of the species (i.e. at about 60 mm) as in the specimen GSC Cat. 77099.

In the specimen GSC Cat. 17251 of the var. *incrassata*, the earliest preserved whorl fragment (a rubber mould) of the second *Euryptychites*-like growth stage (Pl. 39, figs. 3C-3E) has the terminal diameter of about 45 mm with the height-width ratio of only 66 per cent. Its flanks and venter are approximately evenly arched throughout and are separated by a narrowly rounded umbilical shoulder from the markedly convex, obliquely oriented umbilical wall. Therefore, this growth stage begins considerably earlier in the var. *incrassata* than it does in the typical variant of the species. It extends over the next two whorls (incompletely preserved) of the GSC Cat. 17251 (Pl. 39, figs. 3A-3C) to its terminal shell diameter of about 80 mm. Their cross-section is typical of the stage (including broadly rounded umbilical shoulder), except near the oral end where it becomes rounded-trapezoidal with a broadly rounded ventral shoulder separating the flanks from the less markedly arched venter (Pl. 39, figs. 3B, 3C). The height/width ratios vary between 68 and 71 per cent. A living chamber occupies the oralmost part beginning with the shell diameter of about 79 mm (Pl. 39, fig. 3A). Its intermediate nature is suggested by the phragmocone extending to the oral end of the lectotype of the species and the GSC Cat. 77102 with terminal diameters of about 150 mm. Furthermore, the oralmost sutures of GSC Cat. 17251 are simply denticulated, do not exhibit any overlap and but little approximation, contrary to the oralmost adult sutures of GSC Cat. 77102.

The *Euryptychites*-like cross-section of the approximately equivalent, last preserved whorl of the holotype of *S.* (*P.*) *m.* var. *incrassata* (Pavlow, 1914, Pl. VI, figs. 2a, 2b) differs from that of GSC Cat. 17251 only in being subequally arched all over (i.e. without a discernible ventral shoulder) and in having a height/width ratio of only 65 per cent. These morphological distinctions are thought to be infraspecific in character.

Pavlow's (1914, Pl. VII, figs. 1b, 1c) figures indicate that the typically developed second *Euryptychites*-like growth stage extends over the last two wholly septate whorls of the lectotype of *S.* (*P.*) *middendorffi* to its oral end where one can infer the height/width ratio of about 55 per cent at the shell diameter of about 150 mm. The same is true of the wholly septate, large specimen GSC 77102 (Pl. 36, figs. 2A, 2B) where the second *Euryptychites*-like growth stage extends at least to the shell diameter of about 150 mm. Throughout its last whorl beginning at the shell diameter of about 100 mm, the maximum width is situated at the level of the umbilical shoulder. The moderately convex flanks gradually and almost evenly contract adventrally and grade almost imperceptibly into the broadly and somewhat obtusely arched venter. It is barely possible to recognize the approximate position of the ventral shoulder (Pl. 36, fig. 1B). The narrowly rounded umbilical shoulder is clearly delimited from the moderately oblique, straight to slightly concave and moderately high umbilical wall that forms an angle of 60 to 65 degrees with the plane of symmetry. Because of the obliquity of the umbilical wall, very strong involution (about 90 per cent; estimated), and the great width of the shell, the only moderately involute (about 25 per cent) umbilicus is deep and funnel-like, unlike that of the early whorls typified by GSC Cat. 77100 (Pl. 34, figs. 3A, 3B, 3E; Figure 54d). The thickness of the whorl decreases somewhat from the mid-venter to the umbilical shoulder and its height/width ratio is approximately 56 per cent. This whorl appears to be an adult penultimate one for reasons explained in p. 168. If so, the specimen GSC Cat. 77102 must have had a terminal adult shell diameter in order of 190 to 200 mm. The same must have been true of the complete shell of the lectotype of the species (Pavlow, 1914, Pl. VII, figs. 1a, 1c). There is no reason to think that the adult ultimate whorl, a fragment of which is mentioned but neither described in detail nor figured by Pavlow (1914, p. 32), had a differently shaped cross-section. Therefore, and judging by the two above discussed examples, the second *Euryptychites*-like growth stage is a terminal stage extending to the end of the adult ultimate whorl.

Sculpture. The **initial, essentially smooth sculptural stage** was only observed in the GSC Cat. 77100 (Pl. 32, fig. 4; Pl. 34, fig. 3E) where its internal mould is exposed on the early one-third of the second earliest whorl ending with the shell diameter of about 4 mm. The surface of this whorl segment is smooth and lacks constrictions. The smooth appearance of the adumbilicalmost parts of the adjacent whorls visible in the umbilicus suggests that this sculptural stage lasts from the protoconch to the end of the third whorl.

The beginning of the next **Bodylevskites-like sculptural stage** was only observed on a partial internal mould of a fragment of the third or ?fourth earliest whorl preserved inside of the specimen GSC Cat. 17251 of *S.* (*P.*) *m.* var. *incrassata* (Pl. 40, figs. 3D-3F). Its surface bears only a few roundtopped, transversally to subtransversally oriented single ribs (no bundles) and striae which either begin at the mid-flank break or higher up within the preserved upper flank. All ribs cross the venter without weakening. No constrictions were seen. The succeeding main part of this sculptural stage is excellently exposed on the about two-fifths of a whorl long segment of the same specimen (Pl. 39, figs. 3F, 3G). The apparently exclusively trivirgatitpartitous rib bundles of this fragment are remarkably *Bodylevskites*- and *Astieriptychites*-like in their flexuosity, strong forward inclination, refinement and close spacing. The very fine and dense ribs of its adapical part are especially *Astieriptychites*-like (compare Pl. 57, figs. 4E, 4G). However, they become considerably more coarse, more prominent, and more widely spaced toward the oral end of the fragment (Pl. 39, fig. 3F). The fragment is ornamented by about 11 primary ribs, which projects to some 27-28 per whorl. These primaries apparently begin within the outer part of the convex umbilical wall, are straight, and inclined forward at 45 to 50 degrees. The primaries are fine, closely spaced and sharptopped; their strength remains about the same throughout their extent. Most of the primaries bifurcate either within the lower part of the flank or, rarely, just above the umbilical shoulder. The secondary ribs, which are only slightly more delicate and dense than the primaries, bend markedly backward just above the branching point and then turn around to become inclined forward at some 65 to 75 degrees. The anterior secondary remains single while the posterior bifurcates again closely above the first bifurcation point (Pl. 39, fig. 3F). The resulting three supplementary ribs extend across the middle and upper flank on a forward inclined, gently to markedly flexuous course and then cross the venter either subtransversely or with slight but angular forward bend (Pl. 39, fig. 3G). They do not become either weakened or interrupted on the venter. Only a couple of primaries form simple dichotomous bundles and one single rib extends right across one of the flanks and venter in the segment's middle. No constrictions are definitely recognizable. There are about 27 secondaries on the fragment which projects to some 71 per whorl. Neither the beginning nor the end of this typical part of the *Bodylevskites*-like sculptural stage is preserved. The duration of the stage remains uncertain, though it could hardly last longer than two whorls.

The next older **simple dichotomous sculptural stage** is best exposed and typically developed on the last whorl of the GSC Cat. 77100 (Pl. 34, figs. 3A-3D) where it extends from its beginning (at an estimated shell diameter of 27 mm) almost to the end (i.e. to the shell diameter of about 39 mm). The primary ribs of this sculptural stage are high, sharptopped, and have a thin wedge-like cross-section when shell-covered. Their internal moulds are relatively low and roundtopped. There are about 28 primaries per whorl in this stage which is characterized by a gradual adoral widening of roundbottomed interspaces separating them (Pl. 34, figs. 3A, 3B). The primaries begin within the inner half of the umbilical wall as barely distinguishable, thread-like structures and then strengthen gradually all the way to their branching points. They are distinctly inclined backward at first but turn around rapidly on the lowermost flank into a forward inclined direction forming a forward concave, comma-like bend. As a rule, the primaries simply bifurcate either within the lower half of the flank (more commonly) or slightly above the umbilical shoulder (rarely). Only one trivirgatitpartitous bundle was observed. On the flank all secondaries are approximately straight and distinctly forward inclined (at 75 to 80 degrees). Their forward bend increases markedly and progressively on the ventral shoulder where they form broad, forward concave arches. These arches continue across the venter where they become distinctly angular in the middle (Pl. 34, fig. 3D). The secondaries are neither weakened nor interrupted on the venter. The shell-covered secondaries are similar to the primaries in the height, sharptopped appearance, and narrowly wedge-like cross-section while their internal moulds are just as low and roundtopped. However, the secondaries are somewhat more delicate and distinctly more closely spaced than the primaries. There are about 60 secondaries (estim.) per whorl in this sculptural stage. One well defined, roundbottomed constriction occurs in the earliest exposed quarter of the whorl. The oralmost preserved whorl quarter ending at the shell diameter of 42 mm features the alternation of two dichotomous bundles with three trivirgatitpartitous bundles and is interpreted to be a transition to the next following trivirgatitpartitous sculptural stage.

The earliest exposed quarter whorl of GSC Cat. 77099 (Pl. 34, fig. 2A) ending at the shell diameter of about 42 mm is ornamented by simple dichotomous rib bundles entirely similar to those of GSC Cat. 77100. It also represents the end phase of this sculptural stage as the oral half of the whorl is ornamented exclusively by trivirgatitpartitous rib bundles. The same transition between the simple dichotomous and the trivirgatitpartitous sculptural stages is exposed in the specimen GSC Cat. 17251 (Pl. 39, fig. 3E) of *S.* (*P.*) *m.* var. *incrassata* and in the juvenile paratype of *S.* (*P.*) *middendorffi* f. typ. figured by Pavlow (1914, Pl. VII, fig. 2a). As in the GSC Cat. 77099, the more advanced parts of these two whorls are ornamented exclusively by trivirgatitpartitous bundles. Therefore, the simple dichotomous sculptural stage of *S.* (*P.*) *middendorffi* begins in the interval between the shell diameters of 17 and 25 mm, lasts at least through one (?possibly two) of its early whorls, and ends between the shell diameters of 39 and 42 mm. Only in the North Siberian paratype of the species does it appear to end at the shell diameter of about 32 mm.

The presently known examples of the **predominantly trivirgatitpartitous sculptural stage** (see p. 138) are scarce and incomplete. However, they suffice to show that most of its structural details, particularly the degree of refinement and the density of supplementary ribs, vary considerably and like those of *S.* (*S.*) *stubendorffi*. One morphological extreme is the **densely ribbed variant** characterized by a relatively greater refinement and density of supplementary ribs which remain more or less uniform throughout its known extent. This variant, which corresponds to the densely ribbed variant of *S.* (*S.*) *stubendorffi* (see p. 144, 145), appears to be restricted to the typical variant of *S.* (*P.*) *middendorffi*. It is best exemplified by the GSC Cat. 77099 (Pl. 34, figs. 2A, 2B) where it occupies the oral half of the last preserved whorl confined between the approximate shell diameters of 49 and 62 mm. It grades into the simple dichotomous sculptural stage which occupies the early quarter of the whorl, but its end is not reached at its oral end. There are 14 or 15 primaries and 48 to 50 supplementaries on this half-whorl which projects to some 28-30 primaries and 96-100 supplementaries per whorl.

The distinctly backward inclined primary ribs begin within the outer part of the umbilical wall. They form a gentle, forward-convex, comma-like bend on the umbilical shoulder and the lower flank until they become slightly to distinctly inclined forward closely below the first bifurcation point, which is always situated within the lower third of the flank. When shell-covered the primaries and the secondaries alike are attenuated, sharptopped, and markedly elevated but their internal moulds are considerably lower, relatively thickened and roundtopped. The primaries, which are neither distinctly elevated nor appreciably swollen on the umbilical shoulder, are about as attenuated and elevated as the supplementaries in either type of preservation. The concave, roundbottomed interspaces between the primaries are either about as wide as the primaries or up to one and a half times wider than they. The primaries do not become either sparcer or distinctly heavier built adorally to the whorl's end.

The supplementary ribs are either not or only slightly more crowded than the primaries, the width of the primaries' interspaces being either subequal to or only slightly wider than that of the supplementaries. All supplementaries are approximately straight but distinctly forward inclined throughout the middle and upper flank; the anterior one of each bundle being the most prominently inclined. The inclination increases somewhat on the ventral shoulder and they form slight and very broad forward arches on the venter (Pl. 34, fig. 2B) where they are not weakened. Neither the primaries nor the secondaries become noticeably lower, more crowded, or roundtopped adorally.

A considerably greater part of the densely ribbed variant is exhibited on the oral two-thirds of the last whorl of the paratype of the typical form of the species (Pavlow, 1914, Pl. VII, fig. 2a). This interval confined between the shell diameters of about 32 and 46 mm is ornamented almost exclusively by trivirgatitpartitous rib bundles which follow immediately and gradationally the simple dichotomous stage. The primaries and supplementaries of this example of the trivirgatitpartitous stage are similar to those of the GSC Cat. 77099, except in being appreciably finer, more closely spaced, and in having commonly higher bifurcation points. It is the most refined development of the densely ribbed variant known to date.

The late phase of the densely ribbed variant of the trivirgatitpartitous stage was only observed in the earliest exposed one-sixth of the earliest visible whorl of the lectotype of the species (Pavlow, 1914, Pl. VII, fig. 1b) estimated to represent the shell diameter of about 63 mm. This end phase, which is followed by the well developed quadripartitous stage, is essentially similar morphologically to the more coarsely ribbed example of the early phase of the GSC Cat. 77099 (Pl. 34, fig. 2A, B). Judging by these two specimens, the densely ribbed variant of the trivirgatitpartitous stage retains a closely similar morphology throughout its extent. It appears to extend over at least one (probably one and a half to two) intermediate whorls of the typical variant of the species and to be confined approximately between the shell diameters of 32 and 63 mm.

The other extreme of the trivirgatitpartitous sculptural stage — its **sparsely ribbed variant** is typified by the sculpture of the last whorl of the type specimen of *S.* (*P.*) *m.* var. *incrassata* (Pavlow, 1914, Pl. VI, figs. 2a, b). Its earliest exposed part with the shell diameter of about 60 mm is already ornamented exclusively by trivirgatitpartitous rib bundles which extend through its apical half to the shell diameter of about 66 mm before becoming replaced by the quadripartitous sculpture.

All 13 primary ribs preserved on this halfwhorl (projecting to about 26 per entire whorl) are internal moulds. They differ from those of the GSC Cat. 77099 in a distinctly greater length caused by the positioning of the first bifurcation point either at the mid-flank or closely below it. These primaries are distinctly more widely spaced, their interspaces being two to three times wider than they, and distinctly widening upflank. These primaries are also slightly elevated and thickened on and just above the umbilical shoulder, and so slightly bullate. This elevation and thickening increases markedly adorally until the primaries are transformed into low, roundtopped, and comma-like bullae at the stage's end. The comparatively attenuated and lower supplementaries are somewhat inclined forward on the upper flank but cross the venter subtransversally. They are neither weakened nor interrupted on the venter.

The beginning of the sparcely ribbed variant of the trivirgatitpartitous stage is exposed on the fragment of an intermediate whorl (a rubber mould) of the GSC Cat. 17251 (Pl. 39, fig. 3D, 3F) of var. *incrassata*. The entire length of this fragment confined between the estimated shell diameters of 35 and 40 mm exhibits an alternation of trivirgatitpartitous bundles with the subordinate simple dichotomous bundles. Their high and sharptopped primaries, which are twice as thick as the supplementaries, are already distinctly thickened (i.e. bullate) on the umbilical shoulder and the lower flank, unlike the equivalent primaries of the densely ribbed variant. These primaries and supplementaries are generally similar to the more advanced equivalent ribs of the holotype of the variant (Pavlow, 1914, Pl. VI, fig. 2a), except for being somewhat finer and slightly more closely spaced. Furthermore, the supplementaries cross the venter almost exactly transversally, in spite of being distinctly inclined forward on the ventral shoulder.

The combination of the earliest (GSC Cat. 17251) and the late (Pavlow, 1914, Pl. VI, fig. 2a, b) phases of the sparcely ribbed variant of the trivirgatitpartitous stage suggests that it extends over one and a half to two intermediate whorls and that its early and late phases are closely similar morphologically. The sparcely ribbed variant appears to be restricted to S. (*P.*) *m.* var. *incrassata* while the densely spaced variant is only known to occur in the typical variant of the species.

The trivirgatitpartitous sculptural stage is followed immediately and gradationally by the **quadripartitous sculptural stage**, just as it does in *S.* (*S.*) *stubendorffi* (p. 146, 147). The latter stage is only known in three partial examples which represent nevertheless the two morphological variants differentiated in *S.* (*S.*) *stubendorffi*.

The best example of the **predominantly bidichotomous** variant of this stage is provided by the oralmost preserved half whorl of the GSC Cat. 17251 (Pl. 39, figs. 3A, 3B) which includes about 15 mm long initial segment of a presumably intermediate living chamber (see p. 164 for further details). This half whorl is ornamented by 12 primary structures, and by about 45 supplementary ribs which projects to about 24 primaries and about 90 supplementaries per whorl. Neither the beginning nor the end of this sculptural stage is reached on this half whorl.

The primary structures, which are all internal moulds, are inclined at 40 to 50 degrees backward at their beginning on the inside of the umbilical shoulder. Their gradual turn around into a slightly forward inclined position on the umbilical shoulder and lowermost flank results in a comma-like, forward concave shape. These rather short primaries, which bifurcate either within the lowermost one-fifth to one-quarter of the flank or just above the umbilical shoulder, are only slightly to moderately thickened and elevated (i.e. bullate) on the outside of the shoulder and on the lowermost flank. This thickening and elevation increase gradually oralward, the two or three apicalmost primaries being barely bullate while the oralmost three or four are markedly elevated, oval bullae.

In either 5 or 6 bundles out of 12 both secondaries bifurcate again at the same level (either almost immediately or within the lower half of the flank) producing regularly bidichotomous bundles. Quasibidichotomous bundles are less common. Some of the dichotomous elements are only indistinctly attached to their primaries but no general weakening of the sculpture occurs anywhere. At least four regular trivirgatitpartitous bundles and a few single or dichotomous intercalated ribs devoid of primaries are intercalated with the bidichotomous bundles. All supplementary ribs are internal moulds, which are low, narrowly roundtopped, and only half as wide as the most slender, apicalmost primaries. Their shallowly concave interspaces are about twice as wide as they. The thickness of the supplementaries and the width of their interspaces remain constant throughout. No constrictions were noted. All supplementary ribs are distinctly inclined forward and either slightly flexuous or approximately straight on the flank. The inclination of ribs increases on the venter but they cross the venter almost to exactly transversally and are neither weakened nor interrupted there.

The oralmost half whorl of the holotype of *S.* (*P.*) *m.* var. *incrassata* (Pavlow, 1914, Pl. VII, fig. 2a, b) exhibits another example of the predominantly bidichotomous variant of the quadripartitous sculptural stage which matches very closely that of the GSC Cat. 17251, except for a considerably less distinct definition of the bundles (an imperfect reproduction?). Unlike the latter, the holotype exhibits a gradational transition to the preceding trivirgatitpartitous sculptural stage. The two stages do not show any sculptural contrast. Their supplementary ribs are, in particular, indistinguishable in their appearance and spacing.

The **variegated variant** of the predominantly quadripartitous sculptural stage was only observed in the oral five-sixths of the earliest exposed intermediate whorl of the lectotype (Pavlow, 1914, Pl. VII, fig. 1b). Its apical one-sixth exhibits the end phase of the trivirgatitpartitous stage (see p. 166). This example of the quadripartitous stage confined between the shell diameters of 63 and 83 mm features an alternation of various quadripartitous bundles among which the quadrivirgatitpartitous and the quadrifasciculate are prevalent. The primary and supplementary ribs are considerably more refined and crowded and the primaries are distinctly less swollen and elevated than their counterparts in the previously discussed bidichotomous variant of the quadripartitous stage.

The duration of the predominantly quadripartitous sculptural stage remains uncertain, except that it extends almost over an entire whorl in the lectotype of the species. Similarly to the trivirgatitpartitous stage, its predominantly bidichotomous variant appears to be restricted to *S.* (*P.*) *m.* var. *incrassata* while its variegated variant is only known in the typical form of the species.

The next, and the last known sculptural stage was observed in the last preserved whorls of the GSC Cat. 77102 and the lectotype. In the GSC Cat. 77102 (Pl. 36, fig. 2A, B), which typifies this **adult, largely smooth sculptural stage** (see p. 139), the sculpture is strongly weakened on the flank of the earliest part of its last, and only exposed whorl with the shell diameter of about 105 mm. All distinctly elevated, roundtopped, and broadly oval umbilical bullae (internal moulds only) are short, strongly forward inclined, and restricted to the lowermost flank. The umbilical wall appears to be smooth. All rib bundles faintly visible on the flank of this segment seem to be either bidichotomous or quasifasciculate. The still prominent upper parts of supplementary ribs on the uppermost flank and barely delimited venter are similar to those of the preceding predominantly quadripartitous stage, except for being distinctly more sparce and heavier; they cross the venter exactly transversely. This sculpture persists oralward for almost one-half whorl to a well defined and broad, forward inclined constriction (Pl. 36, fig. 2A). Then on the next quarter-whorl the flanks become smooth, except for occasional, disorganized and faint wrinkles, and the adventral parts of the supplementary ribs become faint and only sporadically present. Only the umbilical bullae persist unchanged onto this part of the whorl. Finally, the oralmost quarter-whorl, which is completely septate, is devoid of any sculpture on its well preserved flanks and venter. The bullae probably persist right to whorl's end at the shell diameter of about 150 mm but their presence there is questionable because of a poor preservation of the adumbilical zone. The entire whorl is estimated to carry about 20 bullae.

The description and figures of the lectotype of S. (*P.*) *middendorffi* (Pavlow, 1914, p. 31-33; Pl. VII, fig. 1a, 1c) show that the adult sculptural stage occupying all of its last, entirely septate whorl differs only slightly from that of the GSC Cat. 77102. The prominent umbilical bullae and the upper parts of the supplementary ribs persist to its oral end at the estimated shell diameter of 150 mm. The discernible but somewhat more weakened rib bundles on the flank persist to the shell diameter of about 110 mm. Finally, this whorl bears one relatively more weakly developed constriction.

Pavlow (1914, p. 32) notes the existence of an unfigured ventral fragment of the next following whorl of the lectotype but does not say whether or not it is septate. This is likely to be a fragment of an adult living chamber because the entirely septate last whorls of the GSC Cat. 77102 and the lectotype appear to be nearly complete adult penultimate whorls. A weakening and then the loss of the sculpture similar to that occurring on them is confined to the adult penultimate and/or adult ultimate whorls in many ammonite taxa. Furthermore, at least the last whorl of the GSC Cat. 77102 exhibits strongly approximated to interlocking, obviously advanced adult or terminal external suture lines (see below).

External suture line. Fragments of early juvenile suture lines visible on the imprint of a fragment of the earliest known whorl of the specimen GSC Cat. 17251 (Pl. 40, figs. 3D-3F) and on the exposed part of the earliest whorl segment of the GSC Cat. 77100 (Pl. 32, fig. 4) are too incomplete to be analyzed in detail. However, they do not seem to differ materially from the corresponding elements of the early juvenile sutures of S. (*S.*) *stubendorffi* described and figured by Klimova (1981, p. 78, 79; Figures 3-16 to 3-25 inclusive). No sutures of S. (*P.*) *middendorffi* were either described or figured previously to the best of the writers' knowledge.

The earliest well preserved, complete external suture line occurs in the specimen GSC Cat. 77100 at the shell diameter of about 35 mm (Pl. 34, figs. 3A, 3D, 3E; Figure 55b). According to the shell size, this suture is approximately equivalent to that observed in the specimen GSC Cat. 77111 of S. (*S.*) *stubendorffi* (Figure 52a). The two are also morphologically similar in most respects and the suture of S. (*P.*) *middendorffi* appears to differ only in:

1. Distinctly sturdier (i.e. relatively shorter and wider) proportions of the ventral lobe and both lateral lobes;
2. Relatively lesser size of the third auxiliary lobe combined with its positioning considerably farther away from the umbilical seam (i.e. a greater width of the sixth lateral saddle); and
3. Distinctly more complex denticulation of all its lateral (but not the auxiliary) elements.

These morphological distinctions appear to be rather trivial in themselves. However, the two sutures differ much more substantially in representing different ontogenetic stages. That of S. (*S.*) *stubendorffi* (Figure 52a) does not differ from its late adult sutures (compare Figures 52b, 52c, 53b) in the number and arrangement of its lobes and so is an early adult suture. However, the approximately equivalent (i.e. according to the shell size) suture of S. (*P.*) *middendorffi* (Figure 55b) differs from its adult suture (compare Figures 56a, b) in the presence of only two auxiliaries on the umbilical wall and so remains a juvenile suture.

Three more advanced external sutures have been recorded on the intermediate whorls of S. (*P.*) *middendorffi* which are considerably larger than the whorl where the suture of GSC Cat. 77100 occurs. The first is a well preserved and complete suture exposed at the estimated shell diameter of 75 to 80 mm in GSC Cat. 17251 (Jeletzky, 1965b, Text-figure 1f; this paper, Pl. 39, figs 3A-3C; Figure 55c) of S. (*P.*) *middendorffi* var. *incrassata*. It is neither a far advanced nor a terminal adult suture, in spite of its being followed by the apicalmost part of a living chamber (see p. 164 for reasons). This suture line is indistinguishable from that of the GSC Cat. 77100 (Figure 55b), except in a considerably sturdier and adapically tapering appearance of the first and second auxiliary lobes in the suture of GSC Cat. 17251 and in its third auxiliarly lobe being ill-formed and indistinctly differentiated from adjacent, simply notched, tiny lobules. These distinctions do not appear to be either ontogenetically or subspecifically significant. The imaginary line joining the tops of the lobes of the GSC Cat. 17251 suture ascends slightly (at some 10 degrees) and evenly through its lateral part. Then it turns around within the third lateral saddle to become equally slightly and evenly descendant (or retractive) and retains this orientation to the umbilical seam.

The external suture line visible on the comparably large shell (about 66 mm diameter, estim.) of the lectotype of S. (*P.*) *middendorffi* was not drawn and was only very briefly described by Pavlow, who states (1914, p. 32; Jeletzky's translation from Russian): "The suture line, which is very well visible on the intermediate whorl, is generally speaking similar to the suture line of *P. stubendorffi*. However, its saddles are wider and less denticulated while the terminal prongs of the lobes are shorter." All these features are clearly visible in Pavlow's (1914,

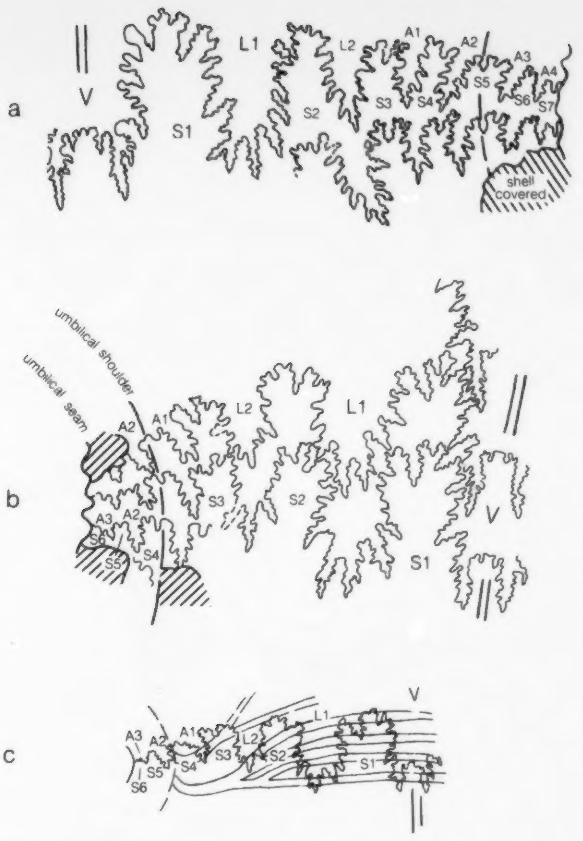


Figure 55. External suture lines of *Siberiptychites*. **a**. *S*. (*S*.) *fascicostatus* n.sp. Early? adult sutures of the holotype. GSC Cat. 17247 reproduced in Pl. 35, fig. 2 at the approximate shell diameter of 52 mm. **b**. *S*. (*P*.) *middendorffi* (Pavlow 1914). Early juvenile suture of the typical variant. Specimen GSC Cat. 77100 reproduced in Pl. 34, fig. 3 at the approxim. shell diameter of 35 mm. **c**. *S*. (*P*.) *middendorffi* (Pavlow 1914). Advanced juvenile suture of its sturdy var. *incrassata* (Pavlow 1914). Specimen GSC Cat. 17251 reproduced in Pl. 39, fig. 3 at the estimated shell diameter of 75 to 80 mm. All figures x 1 (approximately).

Pl. VII, fig. 1a) photograph which shows, in particular, that the strongly adventrally inclined first auxiliary lobe is situated on the adumbilical part of the flank just as in the previously discussed suture line. Furthermore, this auxiliary and the second and first laterals are comparably short and sturdy but distinctly less denticulated than their equivalents in the Canadian representative of *S*. (*P*.) *m*. var. *incrassata* (Figure 55c). Finally, these lobes appear to taper even stronger adapically than their equivalents in this specimen. The intervening second and third lateral saddles of the lectotype appear to be only slightly wider than the equivalent saddles of the Canadian specimen (compare Pavlow, 1914, Pl. VII, fig. 1a with Figure 55c of this paper). Once again, these distinctions do not appear to be either ontogenetically or subspecifically significant.

Most of the above mentioned diagnostic features are equally characteristic of the almost complete external suture lines of the comparably large holotype of *S*. (*P*.) *m*. var. *incrassata* (compare Pavlow, 1914, Pl. VI, fig. 2c with the Figure 55c of this paper). However, as pointed out by Pavlow (1914, p. 33; Jeletzky's translation from Russian) this suture: "also differs somewhat; its outer (i.e. ventral; writers' remark) saddle is noticeably more narrow while the first and second lateral lobes are wider and their median accessory elements are considerably shorter than in the typical representatives of this species." These distinctions are clearly visible in Pavlow's (1. cit.) photograph and attest to the existence of a considerable range of variation in the width of lobes and saddles in these more advanced sutures of *S*. (*P*.) *middendorffi*. This drawn suture line does not include the third auxiliary lobe (see Pavlow, 1914, Pl. VI, fig. 2c). However, there is just enough room for it in the empty, presumably shell-covered interval that separates the median lobule of the fifth lateral saddle from the umbilical seam.

These three sutures of *S*. (*P*.) *middendorffi* are similar to the considerably less advanced (i.e. judging by the relative size of their whorls) suture of the specimen GSC Cat. 77100 in the bulk of their morphological features. The latter suture appears to differ only in an appreciably lesser depth and complexity of denticulation of its elements (especially the lateral ones) combined with a considerably larger size of its adventral part consisting of the ventral lobe, the first lateral saddle, and the first lateral lobe in comparison with its remaining more adumbilical elements. These minor distinctions are attributed exclusively to the earlier age of the suture of GSC Cat. 77100. These three more advanced suture lines of *S*. (*P*.) *middendorffi* are also similar to the advanced to terminal adult external sutures of *S*. (*S*.) *stubendorffi* in most of their morphological features. The two appear to differ only in:

1) Relatively shorter and wider proportions of all lobes of *S*. (*P*.) *middendorffi* which are only 2 to 2.5 times longer than wide. The lobes of *S*. (*S*.) *stubendorffi* are, as a rule, 3 to 4.5 times longer than wide (i.e. when measured across the stem); and
2) An appreciably lesser degree of denticulation of all their lobes and saddles, which are for the most part (excepting the ventral and the first lateral lobes and the first lateral saddle) either simply and shallowly denticulated or only notched in *S* (*P*.) *middendorffi*.

The previously claimed (Pavlow, 1914, p. 32) relatively lesser width of the saddles in *S*. (*P*.) *middendorffi* does not appear to be a constant distinction. It holds true for some of its examples where the saddles are either about as wide as (sometimes even more narrow than) or no more than 1 1/2 times wider than the preceding lobes (e.g. Pl. 39, figs 3A-3C; Figure 55c). These saddles do contrast with the late adult to terminal saddles of most Canadian representatives of *S*. (*S*.) *stubendorffi* (e.g. Pl. 36, figs 1B, 1E; Pl. 54, fig. 1A; Figures 52b, 52c, 53a, 53b) which are two to three times wider than the preceding lobes. However, most saddles (except for the third lateral) of the lectotype of S. (S.) *stubendorffi* (Pavlow, 1914, Pl. VI, fig. 2c), which are exceptionally narrow for the species (see p. 150 for further details), are appreciably more narrow than their equivalents in the holotype of S. (*P.*) *middendorffi* var. *incrassata* (Pavlow, 1914, Pl. VI, fig. 2c) and the above mentioned Canadian representatives of the species. This indicates that the width of the saddles of the two species varies strongly and overlaps considerably.

As with the earlier suture of the specimen GSC Cat. 77100, these three more advanced sutures differ from the adult suture of *S.* (*P.*) *middendorffi* (compare Figures 56a, b) in the presence of only two auxilliaries on the umbilical wall. Hence, unlike the latter, they all are late juvenile sutures.

The adult external suture of S. (*P.*) *middendorffi* is only known in its larger specimen GSC Cat. 77102 (Pl. 31, Figs. 2A-2C; Pl. 36, Figs 2A, 2B; Figures 56a, b) and in another only tentatively identified representative (Figure 57b).

The suture of GSC Cat. 77102 occurs in the middle of its oralmost preserved, entirely septate, apparently adult penultimate whorl. It is inferred to be situated about one-half whorl before the oral end of the adult phragmocone.

The poorly exposed ventral lobe (Pl. 31, fig. 2A; Pl. 36, fig. 2B) and the first lateral lobe are subequally long and about equally intricately and deeply denticulated. Their long and slender first order lobules are ornamented by shorter, second order lobules which are, in turn, shallowly notched.

The first lateral saddle is about as wide as the ventral lobe but about 1 1/2 times wider than lateral lobe. Its top bears two large, first order lobules which are as deeply and complexly denticulated as those of adjacent lobes.

The first lateral lobe is a slender (about 3 times longer than wide), approximately parallel-sided, almost symmetrically trifid structure.

The second lateral saddle is somewhat wider than the first lateral lobe but about 2 1/2 times wider than the second lateral lobe. Its denticulation is similar to that of the first lateral saddle.

The second lateral lobe is a slightly adapically tapering, almost regularly trifid structure that is about as slender as the first lateral but only about 3/4 as long. It is just as deeply and complexly denticulated as the first lateral lobe.

The third lateral saddle occupies the inner one-third of the flank and all of the umbilical shoulder (Pl. 31, fig. 2B; Pl. 36, fig. 1A; Figure 56a), is 3 to 3 1/2 times wider than the second lateral lobe and about twice as wide as the second lateral saddle. Its top is more complexly and deeply denticulated than the flanks of adjacent lobes.

The first auxiliary lobe is situated entirely on the outer umbilical wall (Figures 56a, b). It is a parallel-sided, symmetrically trifid structure that is just as deeply and complexly denticulated as the preceding lobes. Its length is about 2/3 that of the second lateral lobe but it is proportionally longer and more slender (about 5 times longer than wide) than that lobe.

The fourth lateral saddle, which is still situated on the outer half of the umbilical wall, is a very narrow, almost slit-like structure which is not wider than the first auxiliary lobe and is subdivided by a single lobule. Contrary to the preceding saddles, it is almost crossed by the lobules of the flanking lobes (Figure 56b).

The second auxiliary lobe is situated just past the middle of the umbilical wall. This slender and long (about 5.5 times longer than wide), parallel-sided lobe is only relatively simply denticulated by short, occasionally notched lateral lobules and is quite irregularly pronged at the tip.

The fifth lateral saddle, which is situated within the inner half of the umbilical wall, is a diminished carbon copy of the fourth lateral saddle, except that the solitary lobule subdividing its top is an almost simple, slightly trifid structure.

The third and last auxiliary lobe is shaped like the second auxiliary but distinctly sturdier (its length/width ratio is about 4) and distinctly inclined adventrally. It is about two-thirds as long and about one-half as wide as the second auxiliary but is similarly deeply and complexly denticulated.

The exposed ?two-thirds of the sixth lateral saddle separating the third auxiliary from the umbilical seam is about two times wider than the fifth saddle and more complexly denticulated than the latter. No part of the fourth auxiliary lobe is exposed in the few examples of this saddle available (Figure 56b).

The lateral part of the suture line, including its third lateral saddle, is ascendant at 5 to 10 degrees while its umbilical part is subradial to exactly radial (Pl. 36, fig. 1A).

The lobes and saddles of adjacent external sutures of GSC Cat. 77102 are touching extensively and overlap locally. This confirms their being situated close to the oral end of the adult phragmocone.

The adult external suture line of *S.* (*P.*) cf. or aff. *middendorffi* (GSC Cat. 77137; Figure 57a) only differs from that of GSC Cat. 77102 in a few insignificant details attributable to its less advanced age (see p. 173, 174 for further details). Judging by the positioning of this suture on the second adult penultimate whorl, the external suture line of *S.* (*P.*) *middendorffi* becomes adult at least one and a half whorls before the end of the adult phragmocone.

Judging by the two examples of the adult external suture now available, it differs radically from the previously described early and late juvenile sutures. The most important distinctions are:

1. A much deeper and complex denticulation of all its elements which consists of three (in the lateral part)

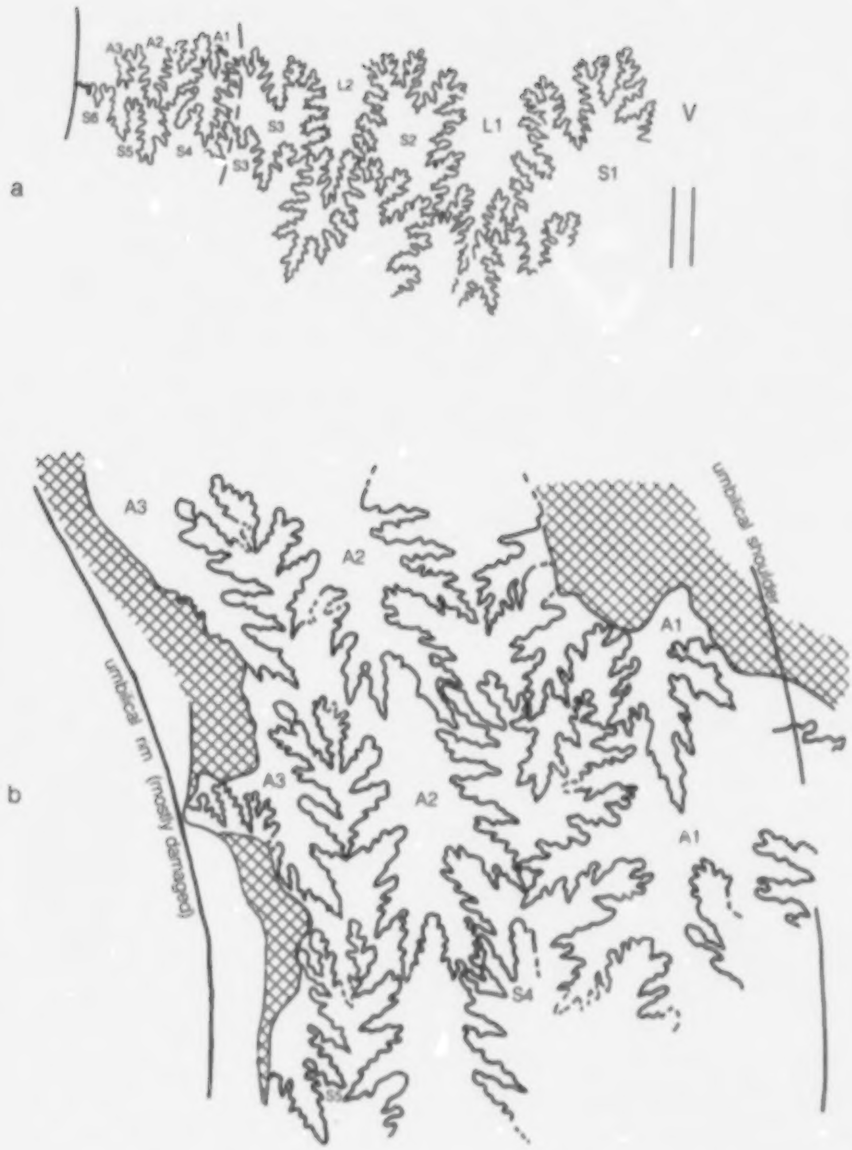


Figure 56. Adult external suture line of *Siberiptychites* (*Pseudoeuryptychites*) *middendorffi* (Pavlow 1914). Specimen GSC Cat. 77102 reproduced in Pl. 31, figs. 2A-2C; Pl. 36, fig. 2A, 2B). **a.** The entire suture line, except for the ventral lobe, X 1. **b.** The umbilical part of the same suture line. Compare Pl. 31, fig. 2C. X 3.

or two (in the auxiliary part) orders of lobules. This distinction is particularly pronounced in the auxiliary parts of these sutures;

2. The extreme attenuation and crowding of all three relatively much larger auxiliary lobes and their positioning on the umbilical wall.
3. The exceptionally small width of the fourth and fifth lateral saddles, which are almost slit-like proportioned, and their positioning on the outer two-thirds of the umbilical wall; and
4. The exceptionally great width of the third lateral saddle which is 3 to 3.5 times wider than the preceding second lateral lobe and spans the outermost part of the umbilical wall in addition to the ventral shoulder and the inner third of the flank.

The probable evolutionary significance of these pronounced distinctions of the adult external suture from the early and late juvenile sutures is commented upon on p. 162.

Affinities and differences. S. (*P.*) *middendorffi* was previously treated first as a morphological variant of *S.* (*S.*) *stubendorffi* (Jeletzky, 1964, p. 46, 48, explanation of fossil plates; 1965b, Figure 1f) and then as an advanced species of *Siberiptychites* s.str. transitional to *Pseudoeuryptychites* (Jeletzky, 1986, p. 354). However, the very different, entirely *Pseudoeuryptychites*-like morphology of its adult external suture line, a different, almost entirely *Pseudoeuryptychites*-like sequence of ontogenetic stages of the whorl shape, a relatively much larger (again *Pseudoeuryptychites*-like) adult size, and an at first strong decline and then an almost complete loss of sculpture on the adult penultimate and, presumably, adult ultimate whorls necessitate its transfer to the subgenus *Pseudoeuryptychites* (see in its description for further details).

In the present incomplete state of its knowledge combined with an equally imperfect state of knowledge of all other *Pseudoeuryptychites* forms, *S.* (*P.*) *middendorffi* differs from all other *Pseudoeuryptychites* in:

1. The narrowly rounded (instead of angular) character of the umbilical shoulder which lasts throughout the known extent (i.e. including the adult penultimate whorl) of its second *Euryptychites*-like growth stage; and
2. The considerably more narrow (21 to 25 per cent against 29 to 36 per cent), *Siberiptychites* s. str.-like umbilicus which persists throughout the known extent (i.e. including the adult penultimate whorl) of its second *Euryptychites*-like growth stage.

The cross-section of the last two whorls of the typical variant of the species, including the adult penultimate whorl (Pl. 36, fig. 2B), does not become markedly laterally expanded, in contrast to that of other *Pseudoeuryptychites* forms (Pavlow, 1914, Pl. XI, figs 2c, 3; Voronets, 1962, Pl. XLII, fig. 1; Pl. XLIX, fig. 1B; Pl. L., fig. 2; Pl. LI, fig. 1; this paper, Pl. 67, fig. 2B; Figure 54f). Instead, it appears to become relatively more slender than the earlier whorls of the second *Euryptychites*-like growth stage and to have the shape and proportions of the cross-section of the sturdier examples of the intermediate variant of *S.* (*S.*) *stubendorffi*. However, the taxonomic value of this feature remains uncertain so long as no comparably advanced whorls of *S.* (*P.*) *m.* var. *incrassata* are known.

Because of the above mentioned subgeneric distinctions of *S.* (*P.*) *middendorffi* from *Siberiptychites* s.str. there is no need to compare it specifically with any of its representatives. However, it must be pointed out that the *Siberiptychites* (*Siberiptychites*) *stubendorffi*-like appearance of its juvenile external suture line (see p. 168-170 for further details) may cause a misidentification of its early and intermediate whorls with the generally similar equivalent whorls of *S.* (*S.*) *stubendorffi* (especially those of its sturdy variant) and *S.* (*S.*) n. sp. aff. *stubendorffi*. Furthermore, it must be pointed out that the ontogenetic changes of the external suture line of *S.* (*P.*) *middendorffi* are so far reaching that its immature representatives bearing early and late juvenile sutures could have been separated subgenerically, or even generically, from the adult ones bearing adult sutures, except for the incontrovertible evidence that all specimens exhibiting these sutures are consecutive growth stages of one and the same species.

The whorl shape of the *Polyptychites rectangulatus*-like growth stage of *S.* (*P.*) *middendorffi* (e.g. GSC Cat. 77100; Pl. 34, fig. 3E; Figure 54d) is similar to that of the comparably large growth stage of *P. rectangulatus*. Therefore, one has to use such more diagnostic features as the *Siberiptychites* s. str.-like external suture, the presence of constrictions, and the presence of pronounced forward loops of supplementary ribs on the venter to differentiate this growth stage of *S.* (*P.*) *middendorffi* from the similarly sized, true *P. rectangulatus*.

In conclusion, it must be pointed out that *S.* (*P.*) *middendorffi* f. typ. and *S.* (*P.*) *m.* var. *incrassata* may conceivably be dimorphs of the species rather than morphological variants. It is possible, though not very likely in the writers' opinion, that the first part of living chamber preserved in GSC Cat. 17251 (var. *incrassata*) and corresponding to an estimated shell diameter of about 80 mm is not an intermediate but a terminal living chamber. In that case *S.* (*P.*) *middendorffi* f. typ., the two presently known adults of which are septate to a shell diameter of at least 150 mm, would be a macroconch form of *S.* (*P.*) *middendorffi*. The holotype of *S.* (*P.*) *m.* var. *incrassata* is about 80 mm in diameter but is completely septate, so it provides no additional information.

Stratigraphic relationships and age. Specimens GSC Cat. 77100 and 77102 were found in bed 16 of the measured Amund Ringnes Island section of the upper Deer Bay Formation in association with the bulk of the Canadian specimens of *S.* (*S.*) *stubendorffi* (see Kemper, 1977, p. 3, Fig. 3 and pages 151-152). Specimen GSC Cat. 17251 (var. *incrassata*) was found at GSC loc. 37867 on Ellef Ringnes Island in association with the sturdy variant of *S.* (*S.*) *stubendorffi* (GSC Cat. 17244). The remaining specimen GSC Cat. 77099 was found on Axel Heiberg Island in association with the unfigured fragment C-4749/2 of *S.* (*S.*) n. sp. aff. *stubendorffi*. This suggest its contemporaneity with bed 14 of the measured section of Kemper (1977, p. 3, Fig. 3) where most other examples of *S.* (*S.*) n. sp. aff. *stubendorffi* were found.

S. (*P.*) *middendorffi* possibly occurs also in the underlying bed 17 of the measured section on Amund Ringnes Island (Kemper 1977, p. 3, Fig. 3, and page 174 below) where *S.* (*S.*) *stubendorffi* appears for the first time. Therefore, the data now available suggest that *S.* (*P.*) *middendorffi* ranges in the Sverdrup Basin through the same beds as does *S.* (*S.*) *stubendorffi* but also extends above its youngest known occurrence to the top of those Sverdrup Basin beds characterized by *Siberiptychites*. The age of these beds in terms of the international standard stages and northern Eurasian fossil zones was discussed on pp. 151, 152.

The stratigraphic relationships and exact age of the North Siberian type material (Pavlow, 1914, p. 33, Pl. VI, fig. 2; Pl. VII, figs. 1, 2) of *S.* (*P.*) *middendorffi* are unknown. However, the later data of Saks et al., (1963) and Gol'bert et al., (1981, p. 59, Table 4) suggest an association with *S.* (*S.*) *stubendorffi* in the upper part of the latter's time range.

Siberiptychites (*Pseudoeuryptychites*) cf. or aff. *middendorffi* (Pavlow, 1914)

Pl. 66, figs. 1A-1F; Figures 54e, 57b.

Material. One whorl fragment from GSC loc. 91311 on Amund Ringnes Island.

Description. The solitary halfwhorl GSC Cat. 77137 is entirely septate and appears to have the terminal shell diameter of some 120 mm. The oralmost preserved part is inferred to correspond to the posterior parts of the oralmost preserved whorls of GSC Cat. 77102 and the lectotype of *S.* (*P.*) *middendorffi* but the earlier part appears to be younger and to represent the oral part of the second adult penultimate whorl because of the less advanced appearance of the suture line.

The more nearly completely preserved apical cross-section (Figure 54e), is 50 mm high and about 75 mm wide (estimated) with the height/width ratio of about 75 per cent. The whorl itself is about 22 mm thick at the midventer but only about 15 mm thick at the umbilical wall. The same is probably true of the less satisfactorily preserved oral cross-section of the specimen. These two whorl cross-sections resemble closely the equivalent cross-sections of the Canadian specimen GSC Cat. 77102

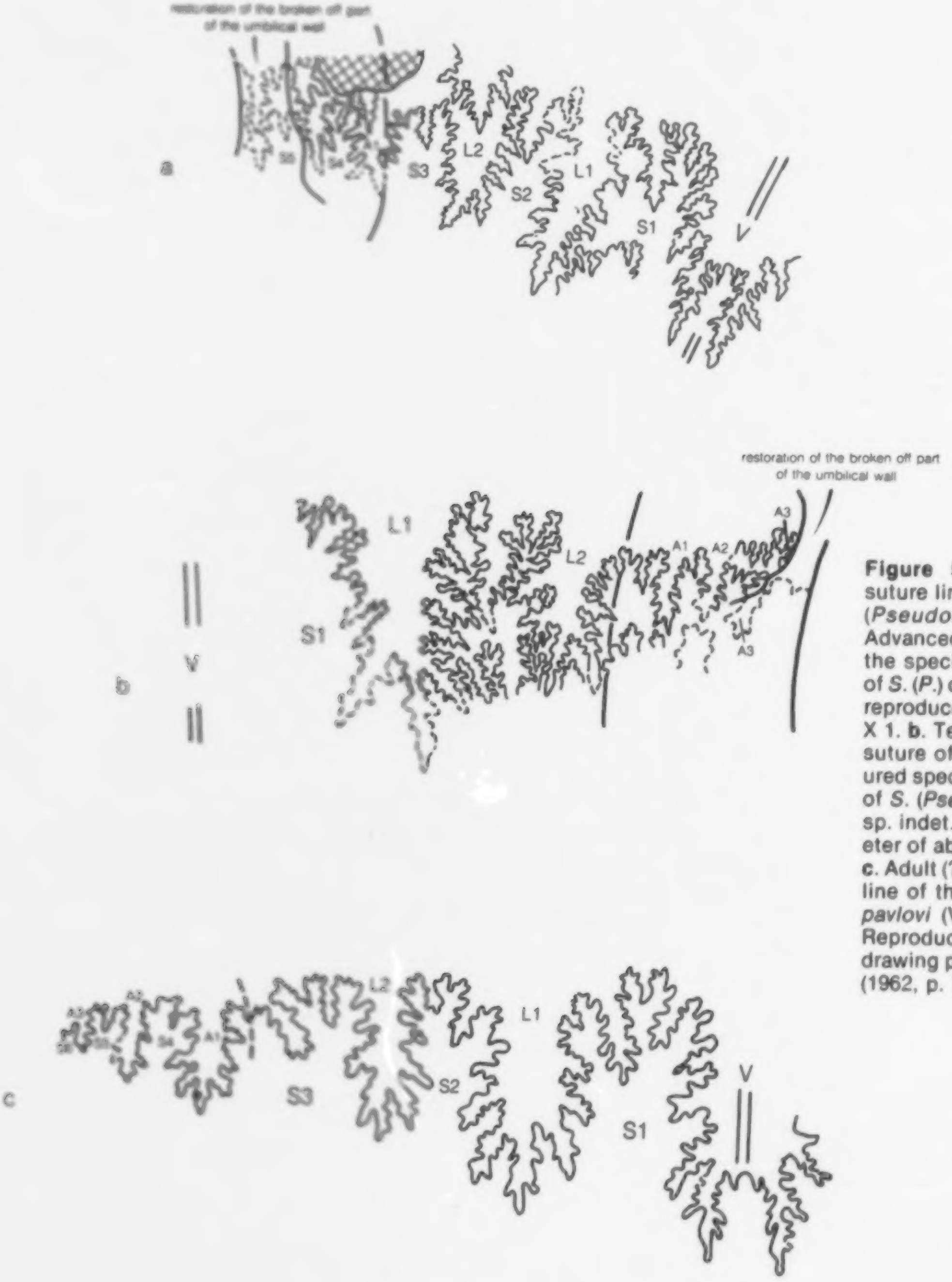

restoration of the broken off part
of the umbilical wall
a
A2
S5
S4
S3
L2
S2
L1
S1
V
restoration of the broken off part
of the umbilical wall
b
L1
L2
A1
A2
A3
S1
V
A3
c
A3
A2
S5
S4
A1
L2
S3
L1
S2
S1
V

Figure 57. Adult external suture lines of *Siberiptychites* (*Pseudoeuryptychites*). **a**. Advanced adult suture line of the specimen GSC Cat. 77137 of *S.* (*P.*) cf. or aff. *middendorffi* reproduced in Pl. 66, fig. 1A-1F, X 1. **b**. Terminal adult external suture of the otherwise unfigured specimen GSC Cat. 79413 of *S.* (*Pseudoeuryptychites*) n. sp. indet. A at the whorl diameter of about 50 mm (est.), X 1. **c**. Adult (?early) external suture line of the lectotype of *S.* (*P.*) *pavlovi* (Voronets, 1962), X 2. Reproduction of the original drawing published by Voronets (1962, p. 79, Fig. 29).

(Pl. 36, fig. 2B) in their narrowly rounded ventral shoulder, only slightly convex, rapidly adventrally converging flanks and the strongly flattened but slightly arched venter that is distinctly delimited from the flanks. However, the flanks are distinctly higher and more narrow than the venter.

The specimen GSC Cat. 77137 also matches closely the Canadian specimen GSC Cat. 77102 of *S.* (*P.*) *middendorffi* and its North Siberian lectotype (Pavlow, 1914, Pl. VII, figs. 1b, 1c) in the degree of prominence, coarseness and spacing of its supplementary ribs on the venter, an almost complete to complete obliteration of the ornament of the flanks, and the feeble development of its apparently subrounded and node-like umbilical bullae. The latter are similarly small, feebly elevated and round-topped in the internal mould preservation at least. The bundling habit is nowhere discernible.

The supplementary ribs ornamenting the imprint of the ventral surface of the preceding intermediate whorl preserved inside of the whorl fragment are indistinguishable from those ornamenting the intermediate whorls of Canadian and North Siberian representatives of *S.* (*P.*) *middendorffi* (compare Pl. 66, fig. 1A with Pl. 34, fig. 2; Pl. 39, fig. 3H). Their bundling habit is not observable.

The somewhat weathered, locally obliterated but almost complete external suture lines visible near the apical end (Pl. 66, figs 1C, 1E, 1F; Figure 57a) are similar to the adult external suture of *S.* (*P.*) *middendorffi* (Figures 56a, 56b), except in:

1. The adjacent sutures being appreciably separated from one another throughout their extent;
2. The third lateral saddle being only one and a half times wider than the second lateral lobe; and
3. The first auxiliary lobe extending onto the umbilical shoulder and the innermost flank.

Affinities and differences. The specimen GSC Cat. 77137 resembles closely the approximately equivalent growth stages of *S.* (*P.*) *middendorffi*. Of the observed morphological differences, those in the details of the external suture line are of an uncertain taxonomic value. The appreciable spacing of adjacent sutures may be attributed to their younger age, the sutures of GSC Cat. 77137 being apparently situated on the oral part of the second adult penultimate whorl which is not represented in our material of *S.* (*P.*) *middendorffi*. The difference in the positioning of the first auxiliary lobe, which is confined to the outermost part of the umbilical wall in *S.* (*P.*) *middendorffi*, may be similarly caused. Finally, the same may be true of the relatively reduced width of the third lateral saddle, which is 3 to 3 1/2 times wider than the second lateral lobe in the more advanced suture of *S.* (*P.*) *middendorffi*. However, the appreciably higher height/width ratio of the whorl (i.e. 75 per cent against 56 to 66 per cent in the approximately equivalent whorls of *S.* (*P.*) *middendorffi* appears to be taxonomically significant. This difference persists throughout the second *Euryptychites*-like growth stage of *S.* (*P.*) *middendorffi* which is represented by several Canadian and Northern Siberian specimens belonging to its typical form and var. *incrassata* (*see* p. 164). The importance of this distinction is increased by the occurrence of the specimen GSC Cat. 77137 in a slightly older bed than the *S.* (*P.*) *middendorffi* found in the Section 11 (see p. 151, 152, 172). Furthermore, ammonites with such a relatively higher cross-section transitional between *S.* (*P.*) *middendorffi* and the ancestral *S.* (*S.*) *stubendorffi* can be expected to occur in such stratigraphic position. Therefore, GSC Cat. 77137 could belong to a new species immediately ancestral to *S.* (*P.*) *middendorffi*. However, the material of *S.* (*P.*) *middendorffi* now available is too scarce to rule out the reference of this specimen to its extremely slender variant which is accidentally absent in the meagre material found in the bed 16 and other Canadian and Northern Siberian localities. The decision about the taxonomic status of the specimen GSC Cat. 77137 is adjurned pending the discovery of a more abundant and better preserved material. In the meantime, it is described in open nomenclature as *Siberiptychites* (*Pseudoeuryptychites*) cf. or aff. *middendorffi*.

From all other *Siberiptychites* (*Pseudoeuryptychites*) species *S.* (*P.*) cf. of aff. *middendorffi* differs in the same way as *S.* (*P.*) *middendorffi* (see its description for further details).

Stratigraphy and age. The only representative of *S.* (*P.*) cf. or aff. *middendorffi* was found in the bed 17 of the section 11 (see Kemper, 1977, p. 3 and p. 151 of this paper). Its occurrence in the lowermost bed of the *Siberiptychites*-bearing sequence of the Deer Bay Formation is rather interesting in suggesting that *S.* (*S.*) *stubendorffi* and *S.* (*P.*) *middendorffi* may have migrated simultaneously into the Sverdrup Basin.

Siberiptychites (Pseudoeuryptychites) pavlovi (Voronets 1962)

Figure 57c

1914	*Euryptychites gravesiformis* Pavlow, p. 37, Pl. XI, figs. 2, 3.
1962	*Euryptychites pavlovi* Voronets, p. 78, 79, Pl. XXXIX, fig. 2; Pl. XL, fig. 2; Pl. XLIX, fig. 1; Figure 29.
1980	*Euryptychites* aff. *pavlovi* Yershova, 1980, Pl. IV, fig. 2.
1986	*Siberiptychites* (*Pseudoeuryptychites*) *pavlovi* Jeletzky, p. 354-356, Figure 38.2.

Type specimen. Voronets (1962) did not designate the holotype of her new species from four specimens available to her. Therefore, the only figured specimen, No. 29a, reproduced in Pl. XXXIX, fig. 2 (where it is erroneously designated No. 25a); Pl. XL, fig. 2; Pl. XLIX, fig. 1 and Text-fig. 29 was formally designated by Jeletzky (1986, p. 356) as the lectotype of *Siberiptychites (Pseudoeuryptychites) pavlovi* (Voronets 1962).

Nomenclatorial status of S. (*P.*) *pavlovi.* "*Euryptychites*" *pavlovi* does not become a homonym of *Polyptychites pavlowi* Koenen 1902 (Pl. I, figs. 1-3), as it was originally assigned to a different genus. Furthermore, the spelling of the two names is different.

Material. No Canadian polyptychitinids definitely assignable to *S.* (*P.*) *pavlovi* (Voronets) are known to the writers. However, Jeletzky's (1986) description is reproduced here with some additions and revisions as the species is the best known representative and the type species of the subgenus *Pseudoeuryptychites*.

Description. The following original description of *Siberiptychites* (*Pseudoeuryptychites*) *pavlovi* is provided by Voronets (1962, p. 78, 79; Jeletzky's translation from Russian): "Whorls are involute, low and thick; the thickness is almost two times greater than the height. Their greatest thickness occurs on the umbilical shoulder. The lateral side is very short and rapidly merges into the wide and flattened siphonal side. The umbilicus is moderately wide, deep and funnel-like shaped. The umbilical shoulder is rounded-acute. The umbilical wall of the inner whorl is covered by primary ribs that begin at the umbilical seam. On its outer whorls these ribs begin in the middle of the umbilical wall. The ribs are fine at first but they become higher as they approach the umbilical shoulder and form the obliquely forward inclined nodes on the latter. There are 16 of these nodes per a complete whorl. The node splits into two secondaries. The anterior secondary is almost of the same size as the node, strongly inclined forward and represents, so to say, the continuation of the node. The posterior secondary is less prominent than the node, splits off the lower part of the latter, and is directed almost radially. An intercalated secondary that adjoins the node may sometimes occur between these two secondaries. These ribs subdivide, in turn, into two branches each. The resulting tertiary ribs are fine and sharp. The distance between them is wider than the thickness of the ribs. There are 8 primary ribs per half whorl; the siphonal side exhibits 44 ribs. The secondary ribs become smooth in the proximity of the nodes as one approaches the living chamber. The distances between the ribs on the siphonal side increase in that direction and then the ribs disappear completely on the living chamber. There are four constrictions on the whorl of which one is very deep and wide. Only a part of the living chamber is preserved.

"The suture line (Fig. 29) is strongly denticulated. The line joining the tops of saddles is oriented almost radially with only its auxiliary saddles being lowered (i.e. descendant). The siphonal lobe is longer than the first lateral one. However, the first lateral lobe is twice as long and wide as the second lateral lobe. The outer (i.e. S1 of Fig. 57c) and the second lateral (i.e. S3 of Fig. 57c) saddles are very wide. The width of the first lateral (i.e. S2 of Fig. 57c) is one-third that of the other two saddles. The second lateral saddle is subdivided into two unequal parts by a long auxiliary lobe.

"*Dimensions (in mm)*

Shell diameter	74(100)
Height of whorl	30(40)
Thickness of whorl	58(78)
Diameter of the umbilicus	32(29)"

This description appears to deal only with the lectotype of the species reproduced in Pl. XXXIX, fig. 2; Pl. XL, fig. 2 and Pl. XLIX, fig. 1, but not with the other three unfigured specimens. Therefore, the range of variability of individual morphological features within the type lot remains unknown. This description is also incomplete in other ways.

First, it does not discuss the ontogenetic changes of shape and proportions of the whorl, which were previously described and clearly illustrated by Pavlow (1914, p. 37, Pl. XI, fig. 2c). According to him, the adult, *Euryptychites*-like habitus of *S.* (*P.*) *pavlovi*, with its uniformly and very low-arched cross-section of the ventral region, the angular umbilical shoulder, and approximately straight umbilical wall, first appears at a shell diameter of 40 to 45 mm. The preceding two whorls have an entirely different, rounded-rectangular to rounded-trapezoidal, only slightly wider than high cross-section with rounded but clearly defined ventral and umbilical shoulders. This cross-section matches closely, and evidently corresponds to, the *Polyptychites rectangulatus*-like growth stage (see the description of the genus *Siberiptychites*). The next younger whorl cross-section, which is about 5.5 mm wide and only about 3 mm thick, is again *Euryptychites*-like in its proportions as well as in the uniformly- and low-arched shape. This cross-section is similar and evidently corresponds to the first *Euryptychites*-like growth stage.

Second, the description of sculpture is incorrect and omits its ontogenetic development. As visible in Voronets' (1962, Pl. XXXIX, fig. 2) photograph, the earliest exposed intermediate whorl with a terminal shell diameter of about 70 mm, is not ornamented by bidichotomous rib bundles alone. Instead, it exhibits an irregular alternation of regularly bidichotomous, subbidichotomous, quadrivirgatitpartitous and quadrifasciculate bundles. The apparently exclusively bidichotomous ornament appears to be restricted to the adapical third of the next older whorl, with a shell diameter of about 76 mm (Voronets, 1962, Pl. XL, fig. 2a). The exact character of bundling is obscured on the oral two thirds of that whorl because of an obliteration of the lower parts of secondary ribs. These parts of ribs become distinct again on the adapical third of the next and last preserved whorl of the lectotype (Voronets, 1962, Pl. XLIX, fig. 1a) with a shell diameter of about 90 mm. However, this oralmost phase of clearly defined ornament is again dominated not by bidichotomous bundles but by true polyptychous bundles, consisting of one trifurcate and one bifurcate branch. On the whole, this ornament is entirely similar and corresponds to the quadripartitous sculptural stage of *Siberiptychites*. The secondary and tertiary ribs are completely detached from the umbilical bullae on the adoral two thirds of the last preserved whorl of the lectotype (Voronets, 1962, Pl. XLIX, fig. 1a, b), which represents the early part of a presumably intermediate (because of the spacing of oralmost sutures; see below) living chamber. Furthermore, the ribs are irregularly spaced and unequally prominent there, in contrast to their regular spacing and equal strength in earlier growth stages. This terminal disorganization of the ornament is similar and corresponds to the terminal sculptural stage of *Pseudoeuryptychites* (see p. 139). The recurrence of these sculptural stages in S. (*P.*) *pavlovi* suggests that its earlier, unexposed whorls bear sculpture similar to that of earlier sculptural stages of *Siberiptychites* s.str.

The inner (second penultimate?) whorl of the specimen of S. (*P.*) *pavlovi* figured by Pavlow (1914, Pl. XI, figs. 2a, b) only differs from its lectotype in an appreciably earlier disorganization of the ornament. Its rib bundles become indistinct at an estimated shell diameter of 50 mm simultaneously with the emergence of the *Euryptychites*-like shape and proportions of the whorl. This earlier, apparently infraspecific, disorganization of the ornament is then followed by its marked but irregular weakening on the living chamber of this specimen (Pavlow, 1914, p. 37, Pl. XI, fig. 2c). The living chamber of S. (*P*) *pavlovi* is also characterized by a marked lengthening of umbilical bullae that may become spike-like (Pavlow, 1914, P. 37, Pl. XI, fig. 3).

Finally, this description omits the most diagnostic features of the adult external suture line of S. (*P.*) *pavlovi*, which are clearly visible in Pavlow's (1914, Pl. XI, fig. 2d) and Voronets' (1962, Figure 29) drawings. This suture, reproduced in Figure 57c, is *Pseudoeuryptychites*-like in the presence of three, well developed auxiliary lobes on the umbilical wall, which are relatively larger, more strongly denticulated, and more crowded in comparison with their *Siberiptychites* s.str. equivalents. The intervening fourth and fifth lateral saddles are correspondingly narrowed. The extremely wide and rather complexly denticulated third lateral saddle spans the umbilical shoulder and much of the inner (or adumbilicalmost) part of the flank instead of being situated entirely on the umbilical shoulder. It contrasts with the much more narrow second and first lateral saddles, of which the second is the more narrow. The lateral lobes and the first and second lateral saddles are deeply and complexly denticulated. The sutures are well separated on the part of the whorl that provided the published external suture of the lectotype (Voronets, 1962, Pl. XLIX, fig. 1). Therefore, this suture is an early adult one and is followed by an intermediate living chamber.

The external suture line of S. (*P.*) *pavlovi* figured by Pavlow (1914, Pl. XI, fig. 2b, d) only differs from that of the lectotype infraspecifically in its generally more slender and more finely and deeply denticulated ventral, first and second lateral, and first auxiliary lobes. The third auxiliary lobe appears to be concealed. There is just enough room for it in the narrow, presumably shell-covered space that separates the second auxiliary lobe from the marked position of the umbilical seam. This suture is also an early adult one as its whorl has a diameter of about 68 mm and is the inner whorl of a much larger specimen that includes the adult living chamber (Pavlow, 1914, Pl. XI, fig. 2c).

Affinities and differences. According to Voronets (1962, p. 81), S. (*P.*) *pavlovi* differs from her S. (*P.*) *pateraeformis* in the greater height of its whorls and their greater thickness. Furthermore, the sculpture of S. (*P.*) *pateraeformis* consists mostly of fasciculate and quasifasciculate rib bundles, and its second lateral lobe is differently shaped. Finally, the umbilicus of S. (*P.*) *pateraeformis* measures 32 to 36 per cent *versus* 29 per cent in S. (*P.*) *pavlovi*. The taxonomic value of differences in the bundling habit and the shape of the second lateral lobe is uncertain. These feautres are variable in S. (*P.*) *pavlovi* and their range of variation in S. (*P.*) *pateraeformis* is unknown. However, the rest of the morphological distinctions appear to be valid and sufficient for a full specific differentiation of these two forms. Furthermore, the two also differ in some other important features not noted specifically by Voronets (1962). As already pointed out, supplementary ribs of S. (*P.*) *pavlovi* are regularly and closely spaced and equally strong on the intermediate whorls but become variably strong, irregularly distributed and variably oriented on the two to three terminal whorls of its adult shell. In contrast, the supplementary ribs of S. (*P.*) *pateraeformis* maintain their regular spacing and equal strength to the end of its phragmocone and on the preserved part of its presumably intermediate living chamber (Voronets, 1962, Pl. LII, fig. 2). Furthermore, these ribs maintain the same character until the oral end of the still larger but fully septate Canadian representative of S. (*P.*) *pateraeformis* (see below). Finally, the supplementary ribs of the lectotype of S. (*P.*) *pateraeformis* become (abruptly?) considerably more sparce and widely spaced on the living chamber as compared with the phragmocone (compare Voronets, 1962, Pl. LI, fig. 1a, b with Pl. LII, fig. 1).

S. (*P.*) *pavlovi* differs from *Siberiptychites* (*Pseudoeuryptychites*) *splendens* Bodylevsky (1968, p. 313, Pl. 72, fig. 1), which is conspecific with *Siberiptychites* (*Pseudoeuryptychites*) sp. nov. indet. of Voronets (1962, p. 80, 81, Pl. XLII, fig. 1; Pl. L, fig. 2; Fig. 30), in its possession of a considerably smaller number of bullae per whorl (16 *versus* 20) and a later appearance of an anguar umbilical shoulder. Furthermore, its bundling habit is dominated by well defined trifurcate and quadrifurcate bundles at similar whorl diameters. Finally, the S. (*P.*) *splendens* differs in the persistence of regularly and evenly spaced S. (*P.*) *pateraeformis*-like supplementary ribbing onto its presumably adult penultimate whorl at least (Voronets, 1962, Pl. L, fig. 2).

Distinctions of S. (*P.*) *pavlovi* from the Canadian *Siberiptychites* (*Pseudoeuryptychites*) n. sp. indet. A are discussed in the description of the latter.

Stratigraphy and age. In northern Siberia, S. (*P.*) *pavlovi* was recorded only from its type-locality 29a and 29a.5 at the northeastern end of Paks Peninsula, Lena-Anabar region of North Siberia (Voronets, 1962, p. 18, 79) and from an unspecified locality on Anabar River (Pavlow, 1914, p. 37). At its type-locality, this species was found in the topmost bed of an approximately 50 m thick unit of dark grey shale with thin interbeds and concretions of very hard, grey, argillaceous limestone. The underlying beds of that unit have yielded S. (*P.*) *pateraeformis*. The rich and allegedly uniform ammonite fauna of this unit was assigned by Voronets (1962, p. 18) to the "*Polyptychites* Zone of the middle Valanginian." Subsequent, more detailed zonations of this interval of the Paks Peninsula profile (e.g. Bassov et al., 1970, Bassov et al. in Saks et al., 1972, p. 42; Zakharov et al., 1974, p. 124-126; Gol'bert et al., 1981, p. 56-59) assign this unit to some part of the regional upper lower Valanginian *Polyptychites michalskii* Zone (earlier *Polyptychites stubendorffi* Zone). However, it is difficult to determine the position of the *S.* (*P.*) *pavlovi*-bearing bed of this unit within the *Polyptychites michalskii* Zone. For some unexplained reason, all above mentioned workers neither cite any of the "*Euryptychites*" (i.e. *Pseudoeuryptychites*) species described by Voronets (loc. cit.) nor offer a correlation of the individual fossiliferous lower Valanginian beds and units (their "pachki") distinguished by them with those recognized previously by Voronets (1962, p. 18). However, the citation of "*Euryptychites*" *gravesiformis* (identification of N.I. Shulgina), from unit XVIII of Zakharov et al. (1974, p. 125) suggests its being correlative, in part at least, with the *S.* (*P.*) *pavlovi*-bearing bed of Voronets (loc. cit.) unit. The Russian workers interpret *Euryptychites gravesiformis* by its North Siberian specimens that are, in the authors' opinion, synonymous with *S.* (*P.*) *pavlovi* (see its synonymy). If so, *S.* (*P.*) *pavlovi* occurs in the basal part of the regional *Polyptychites michalskii* Zone that underlies its main part represented by the units XIX-XX of Zakharov et al. (1974, p. 125). This basal part of the *Polyptychites michalskii* Zone is apparently correlative with the *Thorsteinssonoceras ellesmerense*-bearing beds of the Deer Bay Formation (Jeletzky, 1979, p. 56-58, Figure 8) and so is inferred to be older than any part of its next younger *Siberiptychites*-bearing beds where *S.* (*P.*) *stubendorffi* and *S.* (*P.*) *middendorffi* coexist and other *Pseudoeuryptychites* are unknown. This correlation is consistent with the presence of "*Polyptychites ramulicosta*" (a *Siberiptychites* s.s.?) and "*P.* sp. (ex gr. *stubendorffi*)" in the basal part of the overlying units XIX-XX of Zakharov et al. (1974, p. 124-125). The overlying, *Pseudoeuryptychites*-bearing beds 15 and 14 (Kemper, 1977, p. 3, Fig. 3) of the Deer Bay Formation are younger yet (see in the description of stratigraphy and age of *S.* (*P.*) *pateraeformis* for further details).

The early whorl of *S.* (*P.*) *pavlovi* listed and figured but not described by Yershova (1980, p. 70, Pl. IV, fig. 2) from Spitsbergen is assigned to the upper lower Valanginian regional zone of *Polyptychites ramulicosta*, which is approximately equivalent to the regional Siberian *Polyptychites michalskii* Zone.

Siberiptychites (Pseudoeuryptychites) pateraeformis (Voronets 1962)

Plate 38, figure 2A, 2B

?1914 *Euryptychites globulosus* Pavlow, p. 38, Pl. IX, fig. 1.

1962 *Euryptychites pateraeformis* Voronets, p. 81, 82, Pl. XLVIII, fig. 1; Pl. LI, fig. 1a, b; Pl. LII, fig. 1, Text-fig. 31.

1986 *Siberiptychites (Pseudoeuryptychites) pateraeformis* Jeletzky, p. 358, 359, Pl. 38.1, figs. 1A, 1B.

Type specimen. No type specimen of *Euryptychites pateraeformis* was selected by Voronets (1962) who named this *Siberiptychites (Pseudoeuryptychites)* species. Therefore, Jeletzky (1986, p. 358) has selected the specimen No. 29a.8 reproduced in Voronets (1962) Pl. XLVIII, fig. 1; Pl. LI, fig. 1a, b and Pl. LII, fig. 1 as its lectotype.

Material. Six North Siberian specimens, including the lectotype, used by Voronets (1962, p. 81). One large, fully septate, considerably deformed Canadian specimen GSC 77107 from GSC loc. 91309.

Description. The original description of *P.* (*S.*) *pateraeformis* provided by Voronets (1962, p. 81) is as follows (Jeletzky's translation from Russian): "Whorls involute, low and wide. Width of the outer whorl is almost two times greater than its height. The width of inner whorls is only 1.4 times greater than their height. The greatest width of the whorls occurs at the level of the umbilical shoulder. The surface of the flanks is short and merges immediately into the wide and flattened siphonal side. The umbilicus is wide and deep with a high, abruptly delimited rim (i.e. umbilical shoulder; translator's remark). It is covered by ribs, which bend forward when they cross the shoulder and form forward bent bullae at that level. On the outer whorl, the ribs begin in the middle of the umbilical wall. There are 8 bullae on the inner half of the whorl and there are 15 of them on the whole of the outer whorl. Three fine and high secondary ribs branch off each bulla. The median rib is the continuation of the bulla. The anterior rib separates from its flank and bends forward while the posterior rib splits off the bulla at the umbilical shoulder and is directed radially. Higher up the ribs bifurcate again at the midflank. Intercalated ribs occur locally. All ribs cross the venter on an almost straight course. There are 51 secondaries per one half whorl. The living chamber occupies almost the whole whorl.

"The bullae become more elevated on the living chamber in comparison with the early whorls. However, the secondary ribs become gradually weakened as they approach the mouth border. There are three constrictions per whorl, one of them near the mouth.

"The suture line (Fig. 31) is characterized by a broad, downward widening second lateral lobe and a wide second lateral saddle (i.e. S_3 of this paper) which is situated at the umbilical shoulder.

"*Dimensions (in mm)*

Shell diameter	125(100)	80(100)
Height of whorl	44(37)	32(40)
Thickness (i.e.width) of whorl	84(68)	46(57)
Width of umbilicus	45(36)	26(32)"

The description apparently pertains to the figured lectotype of *P.* (*S.*) *pateraeformis* and one other specimen but takes no account of the remaining four specimens available to Voronets (1962, p. 81). This description also suffers from the incomplete preservation of the lectotype that does not include the adult ultimate whorl, may lack the adult penultimate whorl as well, and does not exhibit early intermediate and juvenile whorls.

Furthermore, the lectotype does not exhibit a complete external suture line.

In spite of these defects, the presence of three constrictions per whorl of the lectotype, in combination with the *Euryptychites*-like morphology of the two exposed intermediate whorls attests that "*Euryptychites*" *pateraeformis* is a representative of the *Pseudoeuryptychites*.

The incomplete and considerably deformed Canadian specimen GSC 77107 (Pl. 38, fig. 2) closely resembles the lectotype of *P.* (*S.*) *pateraeformis* in most of the diagnostic features available. The whorl shape and proportions of its only accessible, last preserved whorl are similar to those of the last preserved, appreciably smaller whorl of the lectotype (estimated ratio height/width about 0.50 and the roughly estimated width of the deformed umbilicus between 30 and 35 per cent). There are about 16 small, pronouncedly forward-bent bullae on this fully septate whorl. Wherever the lower flank is preserved (Pl. 38, fig. 2A), these bullae split into three fine and sharp secondary ribs that are similar to those of *P.* (*S.*) *pateraeformis* in every respect. The intercalated ribs are either rare of absent. Though the supplementary ribs on the venter of this whorl cannot be counted exactly, they are estimated to number between 70 and 80, which compares closely with their number on the last preserved whorl (but not the earlier whorls) of the lectotype (compare Voronets, 1962, Pl. LII, fig. 1). These supplementaries also have about the same degree of thickness, sharpness and elevation and are spaced about as widely as those of the last whorl of the lectotype.

The Canadian specimen GSC 77107 appears to differ from the lectotype of *P.* (*S.*) *pateraeformis* in:

1. Its considerably larger dimensions, the terminal shell diameter being in the order of 135 to 140 mm. The Canadian specimen is septate to the end, strongly suggesting that the living chamber of the lectotype is an intermediate rather than adult living chamber.
2. An apparent absence of the abrupt replacement of the very closely spaced ribbing habit of the penultimate whorl of the lectotype (see Voronets, 1962, Pl. LI, fig. 1a, b) by a much more sparce ribbing habit on its last preserved whorl (see Voronets, 1962, Pl. LII, fig. 1). However, a broken off part of the terminal quarter-whorl on the unfigured flank of our specimen exhibits a considerably more dense ribbing of the oralmost preserved part of the preceding whorl. It is inferred therefrom that the ribbing habit of the earlier inaccessible part of that whorl is similar to that of the comparably large penultimate whorl of the lectotype.

Because of the far reaching morphological similarity of the specimen GSC 77107 to the lectotype of *S.* (*P.*) *pateraeformis*, and the apparently infraspecific nature of their discernible morphological differences, the former is assigned unreservedly to this North Siberian species.

Affinities and differences. The distinctions of *S.* (*P.*) *pateraeformis* from *S.* (*P.*) *pavlovi* and the Canadian *S.* (*P.*) n. sp. indet. A are discussed in the descriptions of these species.

From *Siberiptychites (Pseudoeuryptychites) splendens* Bodylevsky (1968, p. 309, Pl. 72, fig. 1 = *Siberiptychites (Pseudoeuryptychites)* sp. nov. indet. of Voronets (1962, p. 80, 81, Pl. XLII, fig. 1; Pl. L, fig. 2; Figure 30) *S.* (*P.*) *pateraeformis* differs in a considerably lesser number of umbilical bullae per whorl (15 *versus* 20) and in the prevalence of well formed trifurcate rub bundles. The material of this *Siberiptychites (Pseudoeuryptychites) splendens* is scarce, fragmentary and represented mostly by considerably larger, more advanced (including the early part of ?adult living chamber) whorls than the holotype of *S.* (*P.*) *pateraeformis*. Furthermore, its Canadian specimen GSC 77107, which is larger than the lectotype of *S.* (*P.*) *pateraeformis*, appears to be morphologically transitional to the Canadian *Siberiptychites (Pseudoeuryptychites)* n. sp. indet. A. Therefore, the taxonomic significance of above distinctions cannot be evaluated definitively. All three forms are treated tentatively as specifically distinct but may yet prove to be but extreme morphological variants of the same variable species.

The differences of *Siberiptychites (Siberiptychites) pateraeformis* from *S.* (*P.*) *middendorffi* are discussed in the description of the latter species.

Stratigraphy and age. In Northern Siberia *S.* (*P.*) *pateraeformis* is recorded from the Leŋa-Anabar region only. There it occurs in the Valanginian section exposed on the northeastern end of Paks Peninsula (Voronets, 1962, p. 18, 81), at an unspecified locality in the fourth ridge of Prontshistchev Range (Voronets, 1962, p. 18), and at an unspecified locality on Anabar River (Pavlow, 1914, p. 38, Pl. XI, fig. 1). The *S.* (*P.*) *pateraeformis*-bearing beds can be dated and correlated only at its Paks Peninsula locality, where our species occurs in the same unit as, but stratigraphically slightly below, the *S.* (*P.*) *pavlovi*-bearing bed (see in the description of its stratigraphy and age for further details). The bed containing *S.* (*P.*) *pavlovi* appears to represent the basal part of the regional *Polyptychites michalskii* Zone and to correspond to the *Thorsteinssonoceras ellesmerense* beds of the Deer Bay Formation. Therefore, the next older, *S.* (*P.*) *pateraeformis*-bearing beds of the Paks Peninsula section are probably correlative with the upper part (i.e. the *Temnoptychites syzranicus* Subzone) of the next older, regional *Temnoptychites syzranicus* Zone. So interpreted, they would correspond to part or all of the units XVI-XVII of Zakharov et al. (1974, p. 124). If so, these *S.* (*P.*) *pateraeformis*-bearing Siberian beds are correlative with part of (?all of) the *Temnoptychites kemperi*-bearing beds of the Deer Bay Formation (see Jeletzky, 1979, p. 56-58, Fig. 8).

The Canadian specimen GSC 77107 of *S.* (*P.*) *pateraeformis* was found in bed 15 of the Section 3 (Kemper, 1977, p. 3, Fig. 3), which is correlative with the lower, but not the basal, part of *Polyptychites michalskii* Zone (Jeletzky, 1979, p. 56-58, Fig. 8). Furthermore, *Siberiptychites (Pseudoeuryptychites)* n. sp. indet. A was found in the younger bed 14 of that section. These Canadian records appear to be contemporary with the record of "*Euryptychites*" sp. (most likely referable to *Pseudoeuryptychites*) in the topmost bed of units XIX-XX of the Paks Peninsula section (Zakharov et al., 1974, p. 126). Therefore, *S.* (*P.*) *pateraeformis* appears to be a long-ranging species that existed through part or all of the *Temnoptychites syzranicus* Subzone and through the lower part at least of the overlying *Polyptychites michalskii* Zone. In the Sverdrup Basin, *S.* (*P.*) *pateraeformis* has so far been found only in beds that appear to be correlative with the topmost part (i.e. the lower, but not the lowermost, part of the *Polyptychites michalskii* Zone) of its time range. Because of a similarly restricted Canadian time range of *Siberiptychites (Siberiptychites) stubendorffi* (Jeletzky, 1979, p. 56-58, Fig. 8), this discrepancy is explained by a strongly delayed eastward migration of *S.* (*P.*) *pateraeformis* out of its evolutionary center in the Lena-Anabar Basin of Northern Siberia.

Siberiptychites (Pseudoeuryptychites) n. sp. indet. A.

Pl. 46, fig. 1; Pl. 67, fig. 2A, B; Figures 54f, 57b, 58a

1986 *Siberiptychites (Pseudoeuryptychites)* n. sp. indet. A Jeletzky, p. 359, 360, Pl. 38.1, fig. 2A-C; Figures 38.3, 38.4.

Material. Four larger and several small, partly deformed to completely squashed fragments from GSC loc. 93754 (= 91308). All of them were obviously collected from the float.

Description. Only three subgenerically identifiable larger fragments are discussed below. Though conceivably belonging to more than one specimen, they are sufficiently similar morphologically to be conspecific and are so treated here. Other fragments are only tentatively assigned to our form.

The early whorls less than 40 mm high are too strongly deformed to infer their original shape and proportions. The earliest almost undeformed cross-section of the unfigured example GSC 79414 is about 40 mm high and 45 to 50 mm wide. The shape and proportions of this presumably third penultimate whorl are similar to those of comparably large whorls of *Polyptychites keyserlingi* (compare Jeletzky, 1973, Pl. 3, fig. 2b) and the intermediate variant of *Siberiptychites (Siberiptychites) stubendorffi* (compare Pavlow, 1914, Pl. V, fig. 5b; this paper, GSC Cat. 77116; Pl. 44, fig. 1; Pl. 54, fig. 1; Pl. 67, fig. 3). The next older, apparently second penultimate whorl, that comprises the oralmost part of this fragment, has an *Euryptychites*-like shape and proportions. The same is true of the preserved fragments of the adult penultimate and adult ultimate whorls of the specimens GSC 77119 (Pl. 46, fig. 1; Pl. 67, fig. 2A-B) and GSC 79413 (unfigured). The complete cross-sections of these terminal whorls must have been considerably wider than high (height/width ratio in order of 0.60-0.65). The entire ventral region must have been evenly and low arched, with the flanks inseparable from the venter proper. The preserved umbilical shoulder is pronouncedly angular. The approximately straight umbilical wall is high and forms an approximately right angle with the adjacent part of the flanks. The umbilicus must have been moderately involute, deep and funnel-like. The fragments of the adult living chamber apparently represent a shell diameter of 130 to 140 mm.

The earliest visible sculpture on the fourth penultimate whorl of the unfigured specimen GSC 79414 (at a whorl diameter of about 15 mm) consists of closely spaced, fine, nonbullate primary ribs that are slightly inclined forward. They begin on the umbilical shoulder and appear to bifurcate at or near the medial part of the flank. Upper parts of these secondaries are not visible. This sculpture appears to represent the initial, simple dichotomous sculptural stage characteristic of the genus *Siberiptychites* (see p. 137, 138). The ventral surface of the *Polyptychites*-like second penultimate whorl of this specimen is ornamented by regularly and rather closely spaced (their interspaces are about 2 times wider than the ribs themselves) supplementary ribs that cross the venter with slight forward bends. Neither the bundling habit nor the primaries of this growth stage are exposed.

The ventral region of the adult penultimate whorls of the specimens GSC 77119 (Pl. 46, fig. 1) and GSC 79413 (unfigured) are ornamented by fairly sharp and prominent, moderately heavy but rather sparce (the interspaces being 2 1/2 to 3 times wider than the ribs) supplementary ribs, which are considerably coarser than those of the preceding whorl. They cross the venter with slight forward bend. Neither the bundling habit nor the primaries of this growth stage are visible.

The fragmentary oralmost whorls of the specimens GSC 77119 (Pl. 67, fig. 2A, B) and GSC 79413 (unfigured) represent, respectively, the middle part and the very beginning (with a couple of terminal suture lines; see below) of the adult living chamber. They both lack any ornament, except for large but low and round-topped bullae spanning the umbilical shoulder and petering out closely above and below it. The interspaces are about 2 1/2 times wider than the bullae. The surface of the specimen GSC 77119 is, for the most part, appreciably to considerably abraded but that of the specimen GSC 79413 is fairly well preserved.

An early external suture line is visible on the fourth penultimate whorl of the specimen GSC 79414 at an approximate whorl diameter of 15 mm. This suture lacks the ventral and the first lateral lobes (Fig. 58a). Though this suture already includes all three auxiliary lobes typical of the genus *Siberiptychites*, it is *Siberiptychites* s.s. (i.e. *S.* (*S.*) *stubendorffi*-like) rather than *Pseudoeuryptychites*-like. The *S.* (*S.*) *stubendorffi*-like features include fairly simple to very simple and shallow (especially in the third auxiliary) denticulation of all exposed elements, the positioning of the first auxiliary lobe on the flank, the relatively greater width of the fourth lateral saddle (instead of the third characteristic of *Pseudoeuryptychites*), and the relatively small size of all three auxiliary lobes. The suture is, therefore, a late juvenile one. The two terminal external sutures exposed on the specimen GSC 79413 (Fig. 57b) are, in contrast, entirely *Pseudoeuryptychites*-like. Only the first and second lateral lobes of the best preserved last suture are situated on the ventral region. They are separated from the first auxiliary lobe, that is situated entirely on the outermost part of the umbilical wall, by a uniquely wide third lateral saddle, that is at least 2 1/2 times wider than the fourth saddle. The narrow fourth lateral saddle separates this auxiliary lobe from the only partially preserved second auxiliary that occupies the inner part of the outer half of the umbilical wall. Only the fifth lateral saddle and the small adjacent segment of the third auxiliary lobe are preserved, but there is little doubt of the original presence of that auxiliary within the ample expanse of the remaining, deeply eroded, inner half of the umbilical wall. All visible lobes and saddles are similar to those of *S.* (*P.*) *pavlovi* (Fig. 57c) in their shapes and proportions but are more closely spaced (especially the lateral lobes) and considerably more complexly denticulated. This suture either touches, or overlaps with, the second last suture wherever the latter is visible (Fig. 57b). This indicates the adult nature of this fragment of the living chamber.

Affinities and differences. Siberiptychites (Pseudoeuryptychites) n. sp. indet. A differs from *S.* (*P.*) *pateraeformis* in the considerably higher cross-section of its adult ultimate and penultimate whorls. These whorls are also more highly arched, and approximately equally thick throughout (compare Pl. 67, fig. 3B and Figure 54f with Pl. 38, fig. 2B). Furthermore, the adult living chamber of our form is smooth, except for the umbilical nodes, while that of *S.* (*P.*) *pateraeformis* bears irregularly spaced and unequally thick, coarse ribs in addition to differently shaped umbilical nodes. Finally, the coarse, prominent and widely spaced supplementary ribs of the adult penultimate and second penultimate whorls of *S.* (*P.*) n. sp. indet. A contrast less with the fine and closely spaced supplementaries of its earlier whorls than do the equivalent supplementaries of *S.* (*P.*) *pateraeformis*.

Unlike the vanishing ribbing habit of *Siberiptychites (Pseudoeuryptychites)* n. sp. indet. A, the previously regular ribbing habit of *S.* (*P.*) *pavlovi* becomes strongly disorganized on its adult penultimate and second penultimate whorls and this irregular rib pattern persists onto its adult living chamber. Furthermore, *S.* (*P.*) *pavlovi* develops closely but irregularly spaced, unequally sized and partly spinose umbilical nodes on the adult living chamber. Finally, the *Euryptychites*-like advanced whorls of *S.* (*P.*) *pavlovi*, including the adult living chamber, are relatively much lower, wider and thinner than those of *Siberiptychites (Pseudoeuryptychites)* n. sp. indet. A.

Siberiptychites (Pseudoeuryptychites) n. sp. indet. A resembles *S.* (*P.*) *splendens* Bodylevsky (= *S.* (*P.*) sp. nov. indet. of Voronets, 1962, Pl. XLII, fig. 1, Pl. L, fig. 2) in the smoothness of its adult living chamber (except for the umbilical nodes) and in the subequal thickness of its cross-section throughout the whorl's width. However, its living chamber is about 1 1/2 times thicker than that of *S.* (*P.*) *splendens*. Furthermore, the ventral parts of supplementary ribs of its adult penultimate whorl (Pl. 46, fig. 1) are distinctly coarser, more elevated and more widely spaced than those on the adult penultimate whorl of *S.* (*P.*) *splendens* (Voronets, 1962, Pl. L, fig. 2; Bodylevsky, 1968, Pl. 72, fig. 1a, b).

The differences of *Siberiptychites (Pseudoeuryptychites)* n.sp. indet. A from *S.* (*P.*) *middendorffi* are discussed in the description of the latter species.

Because of its morphological distinctions from all other formally and informally named representatives of *Pseudoeuryptychites*, our form is probably a new species. However, it is described in open nomenclature because of the poor and fragmentary preservation of all its presently known examples.

Stratigraphy and age. All known examples of *Siberiptychites (Pseudoeuryptychites)* n.sp. indet. A have been collected at GSC loc. 93754 (= 91308) in bed 14 of the section of the upper Deer Bay Formation measured by E. Kemper (1977, p. 3, Fig. 3) on North Amund Ringnes Island. These youngest known Canadian representatives of the subgenus *Pseudoeuryptychites* are associated with *Siberiptychites (Siberiptychites)* n. sp. aff. *stubendorffi*. The stratigraphy and age of this bed was already discussed in the descriptions of *S.* (*P.*) *pavlovi* and *S.* (*P.*) *pateraeformis*.

Siberiptychites (new subgenus)? n.sp. B

Pl. 37, fig. 3A-3B

Synonymy

cf. 1914 *Polyptychites* cf. *rinnei* Pavlow, p. 21; Pl. III, figs 3a-3c

cf. 1962 *Polyptychites* cf. *rinnei* Voronets, p. 75, Pl. XLIII, figs. 1, 2.

Material. One fragmentary specimen from GSC loc. 91310.

Locality. Upper Deer Bay Formation, GSC loc. 91310 (Ke 74/11/16) Amund Ringnes Island, N.W.T. Section 11 of Kemper (1977, p. 3, Figure 3), bed 16 situated about 249 m stratigraphically below the base of the Isachsen Formation.

Description. The solitary example of *Siberiptychites* (new subgenus)? n.sp. B consists of a mostly undeformed (except for one of the lower flanks being caved in) segment of a moderately sturdy (height/width ratio is about 78 per cent), presumably adult living chamber comprising about one-third of a whorl (Pl. 37, fig. 3A). The whorl is 61 mm high (measured) and about 78 mm wide (estimated) in its better preserved apical cross-section (Pl. 37, fig. 3B) and so must have belonged to a fairly large form with an adult terminal shell diameter in the order of 130 to 140 mm.

The fragmentary living chamber encloses similarly long segments of at least two preceding whorls, which are strongly deformed to completely squashed throughout. Their shape and proportions cannot be evaluated.

The living chamber is rounded-trapezoidal in cross-section with the maximum width situated at umbilical shoulder. The straight flanks converge adorally at about 15 degrees everywhere between the regularly rounded umbilical shoulder and the broadly rounded ventral shoulder. The latter is illdelimited from the flank and the very low arched, obtuse and broad venter (Pl. 37, fig. 3B).

The lower flank merges rapidly into the moderately high, distinctly concave and markedly oblique (forms an angle of about 70-75 degrees with the plane of symmetry) umbilical wall across the broadly rounded but clearly delimited umbilical shoulder.

The exposed umbilical wall of the innermost preserved (second from last) whorl is ornamented by about 10 closely spaced, prominent and sharptopped but thin primary ribs that are pronouncedly backward inclined. These ribs begin at the umbilical seam and extend all across the umbilical wall becoming only slightly more prominent and not thickened to any degree. They just begin to curve into a subtransversal position before disappearing beneath the next whorl.

The umbilical wall of the preserved fragment of the next (i.e. penultimate) whorl is, in contrast, all but smooth, being ornamented only by slightly elevated, fairly thin and very illdefined (in both the shell-covered and internal mould preservation) adumbilical parts of primary ribs. These obliquely backwardly directed primaries begin at or near the umbilical seam. They only begin to strengthen markedly and rapidly on the umbilical shoulder, where they rapidly transform into broadly based, radially elongate bullae that are strongly elevated and sharp-topped in the shell-covered state but are much lower and roundtopped in the internal mould (Pl. 37, fig. 3A). These bullae are comma-like and markedly concave adorally; their tops are concealed beneath the umbilical seam of the ultimate whorl. They are separated by deeply concave, roundbottomed interspaces that are about twice as wide.

The bullate primaries of the ultimate whorl are similar to those of the penultimate whorl, except for being still more prominent on the umbilical shoulder and the lowermost flank and considerably more widely spaced. The shallowly concave interspaces separating them are at least three times wider than their width in the internal mould (Pl. 37, fig. 3A). There are 6 to 7 of these bullae per one-third of the ultimate whorl, which suggests some 19 to 21 of them per whorl. The primaries begin as fine, slightly elevated ridges on the outermost quarter of the umbilical wall, leaving the rest of its smooth to faintly striated. They are pronouncedly backward directed on the outermost umbilical wall and the umbilical shoulder but turn around rapidly on the lowermost flank closely before the branching point. They rapidly increase in height and thickness throughout that interval until they become regular bullae that reach their maximum prominence just before the branching point.

The coarse and sparce supplementary ribs were only observed on the fragment of the last whorl. On its better preserved undeformed flank (Pl. 37, fig. 3A) they number 18 or 19, which suggests some 55 to 60 supplementaries per entire whorl. All supplementaries are either approximately straight or only slightly flexuous throughout their extent on the flank. They are markedly weakened but not interrupted on the mid-flank, which permits one to see the mode of branching. The three to four complete bundles of the figured flank are trifasciculate, with the exception of the apicalmost bundle which is trivirgatitpartitous. In this bundle the anterior secondary bifurcates again somewhat below mid flank. The posterior rib of each bundle is radially to subradially directed with the other two ribs becoming progresively more adorally inclined. At the incompletely preserved last part of the flank there seems to be a dichotomous bundle starting from the bulla and followed by an intercalated secondary. All supplementary ribs cross the venter either transversally or with a faint suggestion of a very broad forward loop. They all become gradually more prominent adventrally and are most prominent on the venter. These broad-based, moderately sharptopped supplementary ribs (in the internal mould) are separated by broadly concave interspaces that are three to four times wider (Pl. 37, fig. 3B).

The external suture line is not observable.

Affinities and distinctions. Siberiptychites (new subgenus)? n.sp. B resembles closely the enigmatic, rather incompletely preserved North Siberian polyptychitinids originally described by Pavlow (1914, p. 22, 23; Pl. III, figs. 3a-3c and Pl. IV, figs. 1a-1c) as *Polyptychites* cf. *rinnei* Koenen 1909 and *P.* cf. *ovatus* Koenen 1909. It resembles equally closely the polyptychitinid forms described and figured by Voronets (1962, p. 74, 75, Pl. XLI, fig. 1; Pl. XLIII, figs. 1a, 1b, 2a, 2b; Pl. XLVIII, fig. 2a, 2b). Of these forms *Polyptychites* cf. *ovatus* Pavlow (1914) non Koenen 1909 and *Polyptychites* sp. nov. indet. of Voronets (1962) differ from the Canadian specimen in a considerably more slender, oval whorl shape, a complete obliteration of supplementary ribs on the mid-flank at comparable whorl diameter and a distinctly more refined and closely spaced appearance of supplementary ribs (especially in the specimens figured by Voronets 1962, Pl. XLI, fig. 1; Pl. XLVIII, figs. 2a, 2b). These specimens are, therefore, believed to be allied to but not conspecific with the Canadian specimen.

The specimen of *Polyptychites* cf. *rinnei* figured by Pavlow (1914, Pl. III, figs. 3a-3c) and those figured by Voronets (1962, Pl. XLIII, figs. 1, 2) are similar to our specimen in nearly every observable feature, including the prevalent mode of bundling. They are, therefore, placed tentatively into its synonymy. As the Northwest German *Polyptychites rinnei* Koenen (1909, p. 70, Pl. XXVIII, figs. 1, 2) is a morphologically dissimilar, evidently specifically and presumably generically distinct form, the Canadian specimen is described herein in open nomenclature. The presence of constrictions in some of the closely allied to probably specifically identical North Siberian forms contradicts the traditional assignment of them all, and consequently of our specimen, to *Polyptychites*. All of them appear to comprise a new subgenus of *Siberiptychites* that differs in the uniquely coarse and widely spaced ribbing habit of its adult last whorl.

Stratigraphy and age. The only fragment of *Siberiptychites* (new subgenus)? n.sp. B was found associated with *Siberiptychites (Siberiptychites) stubendorffi* and *S.* (*Pseudoeuryptychites*) *middendorffi* in bed 16 of Section 11 of Kemper (1977, p. 3, Fig. 3) on Amund Ringnes Island. It forms, therefore, part of the *Siberiptychites*

(Siberiptychites) stubendorffi fauna, the age and correlation of which were discussed in p. 151, 152.

Genus *Astieriptychites* Bodylevsky 1960

Synonymy

1950	*Astieriptychites* Bodylevsky (a manuscript name).
1958	*Astieriptychites* Voronets, p. 22, 24, 25; Pl. 1, fig. 2, 3 (a nomen nudum, expressly credited to Bodylevsky's manuscript)
*1960	*Astieriptychites* Bodylevsky, p. 172, 173, Pl. 39, fig. 1.
1962	*Astieriptychites* Voronets, p. 82, 83.

Type species. Astieriptychites astieriptychus Bodylevsky 1960.

Derivation of name. From the *Olcostephanus* (= *Astieria*)-like bundling habit of advanced whorls.

Diagnosis. Polyptychitinid ammonites the bullate outer whorls of which combine *Polyptychites*-like shape and proportions with a predominantly tri- to sexti-fasciculate (i.e. *Olcostephanus*-like) bundling of supplementary ribs. Either some or all but one of the supplementary ribs of individual bundles are indistinctly attached to their primaries and there are species in which all supplementaries are either indistinctly attached or almost to completely detached from their primaries beginning with early intermediate whorls because of the presence of a semismooth to almost smooth band on the mid-flank of more advanced whorls. Frequent constrictions are almost invariably present. The nonbullate to feebly bullate inner whorls bear very fine and strongly forwardly bent, flexuous ribs arranged in predominantly trivirgatitpartitous bundles. The supplementary ribs are commonly weakened on the lower flank and form pronounced forwardly-convex bends on the venter. The complex, *Siberiptychites*-like alternation of whorl shapes and sculptural stages is absent. The moderately involute to moderately evolute (28 to 35 per cent) umbilicus is markedly step-like.

The external suture line differs from that of *Polyptychites* in a markedly ascendant to subradial orientation of its lateral part and a subradial to slightly ascendant orientation of its auxiliary part. Furthermore, it has three to four auxiliary lobes instead of two to three present in the suture line of *Polyptychites*.

Type area. Central part of North Siberia (Anabar-Khatanga Basin).

Geographical range. North Siberia, Arctic Canada (Sverdrup Basin), Spitsbergen (Yershova, 1980, p. 70, 71; Pl. VI, fig. 1 and "*Neocraspedites*" *mirus* Yershova). Probably present elsewhere in the European Arctic also.

Historical remarks. The Boreal Valanginian polyptychitinids presently assigned to *Astieriptychites* Bodylevsky 1960 were originally described as representatives of *Simbirskites* by Pavlow (1914, p. 41-43; Pl. XIII, fig. 8; Pl. XIV, figs. 1, 2). This worker described the North Siberian type species of *Astieriptychites* — *A. astieriptychus* Bodylevsky 1960 — as *Simbirskites toensbergensis* Weerth. He also described another closely related North Siberian ammonite as *Simbirskites*? *tenuisculptus* sp. nov. In spite of these identifications, Pavlow (1914, p. 43) pointed out that *S. toensbergensis* and *S.*? *tenuisculptus* could only be tentatively assigned a mid-Neocomian (i.e. Hauterivian) age.

Bodylevsky (1939, p. 66), who was the next to study *Astieriptychites*, initially accepted unreservedly Pavlow's (1914) identification of *Simbirskites toensbergensis* in Northern Siberia and dated it as of Hauterivian age. However, he revised his opinion later in a manuscript (Bodylevsky 1950) discussed by Voronets (1958; see below for further details) and a published communication to the Interdepartmental Conference on the Stratigraphy of Siberia (Bodylevsky, 1957, p. 98). In the published communication Bodylevsky (1. cit.) pointed out that the inner whorls of *Simbirskites toensbergensis* Pavlow non Weerth are characterized by a typical *Polyptychites*-like ribbing habit. Consequently, this species was re-determined (but neither described nor figured) as a new polyptychitinid species — *Polyptychites astieriptychus* Bodylevsky.

Bodylevsky (1950) pointed out in the manuscript but not in the published note that *P. astieriptychus* may have to be placed in a new genus *Astieriptychites*. According to Bodylevsky (1957, p. 98) *Simbirskites*? *tenuisculptus* Pavlow 1914 did not seem to be a true *Simbirskites* either. However, he still favored an early Hauterivian age of the beds containing these peculiar ammonities.

The above discussion of *Polyptychites astieriptychus* does not represent a valid publication of either the genus *Astieriptychites* or its type species *A. astieriptychus*, which were only validly published in a subsequent paper of Bodylevsky (1960, p. 172, 173, Pl. 39, fig. 1). This paper was preceded, however, by that of Voronets (1958, p. 22, 24, 25; Pl. 1, figs. 2, 3) where the genus was discussed and named while the species was described, figured and assigned to *Astieriptychites*. Voronets (1. cit.) derived this taxonomic information from Bodylevsky's (1950) manuscript, which remained unpublished but was accessible to her. The use of the name *Astieriptychites* by Voronets (1. cit.) does not affect either the authorship or the date of publication of that genus as she expressly credits Bodylevsky (MS 1950) with its erection. Furthermore, Voronets (1958, p. 22, 24) failed to satisfy the requirements of the Rules of Zoological Nomenclature as she did not provide a diagnosis of *Astieriptychites* or designate a type species. Voronets' (1. cit.) publication does not affect the authorship and the date of publication of *A. astieriptychus* either as this species is expressly credited to Bodylevsky (MS 1950) by her (Voronets, 1958, p. 24). Therefore, the genus *Astieriptychites* and its type species *A. astieriptychus* are considered herein to be validly published in the subsequent paper of Bodylevsky (1960) which does not mention Voronets (1. cit.) paper at all.

The concept and taxonomic status of Astieriptychites. Bodylevsky's (1960, p. 172, 173) original diagnosis of *Astieriptychites* is as follows (Jeletzky's translation from Russian):

"Shell more or less swollen, cross-section of the whorl low and wide, umbilicus is moderately narrow. The suture line as in *Polyptychites*."

"The sculpture of inner whorls consists of trifurcate or quadrifurcate polyptychitid bundles (i.e. in a bundle originating in a primary rib one or two ribs subdivide repeatedly above the bundle's base). These whorls are devoid of nodes at the places where the secondaries arise. The sculpture of outer whorls consists of bent (backwardly convex) nodes, which occur at the umbilical shoulder, and bundles of secondary ribs consisting of several ribs (up to five or six ribs in a bundle). Of the secondary ribs, only one (usually the anterior rib) is firmly attached to the umbilical node. Furthermore, some of the ribs have the character of intercalated (intermediary) ribs. In this growth stage the ribs are feebly bend forward and cross the ventral side without any weakening and bends. The sculpture of the outer whorls resembles that of some *Astieria* (e.g. *Astieria atherstoni*, A. P. Pavlow, 1892, Pl. XVII, fig. 14)."

This diagnosis is incomplete and somewhat misleading in part in the present state of knowledge of *Astieriptychites*. First, Bodylevsky's claim of "moderately narrow" proportions of the umbilicus is invalid. Its width either approaches closely the generally accepted borderline between the moderately involute and moderately evolute proportions (i.e. 33 per cent) or is slightly above that value in all better known representatives of the genus, including its generotype. As known now, the width of the umbilicus fluctuates between 28 and 35 per cent of the corresponding shell diameters in all investigated growth stages of *Astieriptychites*. In combination with the markedly step-like shape of the umbilicus and its moderately deep to shallow proportions, this feature permits a reliable differentiation of *Astieriptychites* from the subgenus *Siberiptychites*, which can no longer be distinguished reliably on their ribbing habits alone. As pointed out earlier in this paper (see p. 152, 157, 158 for further details) and in the following paragraphs of this section, the early and advanced ribbing habits of the latter subgenus may resemble closely those of *Astieriptychites*.

Second, the ornament of the inner whorls of *Astieriptychites* differs markedly from that of equivalent whorls of true *Polyptychites* in a much greater refinement and density of supplementary ribs combined with their pronounced forward inclination on the flank, their marked flexuosity, and their pronounced adoral bends on the venter. Furthermore, these supplementary ribs are commonly weakened in the mid-flank already in these growth stages. These supplementary ribs of *Astieriptychites* resemble closely the equivalent supplementaries of the subgenus *Siberiptychites* and those of the genus *Bodylevskites* in all these respects (see p. 136 for further details).

Third, all supplementary ribs, including the anterior one, may be either indistinctly attached to or almost completely to completely detached from the bullate primary ribs of advanced whorls because of the appearance of a semismooth to almost smooth zone on the middle of the flanks of some Canadian (e.g. *A. obsoletus* sp. nov. and *Astieriptychites*? sp. indet. B; see below) and Spitsbergen (e.g. "*Neocraspedites*" *mirus* Yershova, 1980; Pl. VII, figs. 1a, 3a; Pl. VIII, figs. 1, 3) representatives of the genus.

Fourth, details of ribbing habits of all polyptychitinid genera and subgenera are notoriously variable and fasciculate bundles indistinguishable from those of *Astieriptychites* are by no means absent in representatives of *Polyptychites* (e.g. *P. keyserlingi*; see p. 66, 67 for further details) and *Siberiptychites* s. str. (e.g. *S.* (*S.*) n.sp. aff. *stubendorffi* and *S.* (*S.*) *fascicostatus*). Furthermore, the style of ribbing of advanced whorls of *Astieriptychites* is by no means constant (see Bodylevsky, 1960, p. 173, 174) as some bundles of *A. astieriptychus* and *A. tenuiptychus* exhibit repeated (i.e. *Polyptychites*-like) branching. According to Voronets (1958, p. 25) some adult bundles of *A. astieriptychus* are bidichotomous and the same is true of the Canadian representatives of the genus.

Fifth, though the external suture line of *Astieriptychites* is definitely of a general polyptychitinid type, it differs distinctly from that of all other Polyptychitinae genera and subgenera, including *Polyptychites*. As already noted by Voronets (1958, p. 23; Jeletzky's translation from Russian), this "suture line is peculiar with narrow lobes, broad saddles and three to four auxiliary lobes. Its character is close to that of the suture line of *Dichotomites*." The correctness of this conclusion is illustrated by the drawing of the suture line of *A. astieriformis* provided by Voronets (1958, Pl. 1, fig. 2g). This completely preserved suture, which is erroneously assigned to *A. astieriptychus* in the plate explanation and the title of the description of *A. astieriptychus*, is clearly recognizable as that of *A. astieriformis* because of four well developed auxiliary lobes and other morphological features listed in the description of the latter species (see Voronets, 1958, p. 26, 27). This suture line is all but straight and subradially oriented throughout its extent.

The distinctiveness of the *Astieriptychites* suture line was also recognized by Bodylevsky (1960, p. 174), in spite of his above cited general conclusion to the contrary. He pointed out in the description of *A. astieriptychus*, that this suture and those of other *Astieriptychites* known to him, differ from that of *Simbirskites* in the absence of inversion (i.e. of an adapical bend of its auxiliary part). This feature also distinguishes the *Astieriptychites* suture line from that of *Polyptychites*, which is, mostly, inverted comparably to that of *Simbirskites* (see Pavlow, in Pavlow and Lamplugh, 1892, Pl. XVIII, figs. 4c, 8c, 12b; Wright in Arkell et al., 1957, p.349, figs. 1c, 2c). Bodylevsky (l. cit.) does not mention this distinction of the *Astieriptychites* and *Polyptychites* suture lines and must have overlooked it.

The external suture lines of most *Astieriptychites* species actually differ even more strongly from those of *Simbirskites* and *Polyptychites* than was recognized by Voronets (l. cit.) and Bodylevsky (l. cit.). As pointed out in the description of *A. obsoletus* sp. nov. below (see p. 187, 188), the lateral parts of its adult and late juvenile suture lines (Pl. 49, figs. 2A, 2B; Pl. 62, figs. 2A, 2B;

Figures 58b, 58c) are markedly ascendant while their auxiliary parts are either subtransversally oriented or slightly ascendant. These suture lines have, therefore, a distinctly angular appearance and are knicked in the middle. The incomplete external suture line of *Astieriptychites* species published under the name of *A. astieriptychus* by Voronets (1958, Pl. 1, fig. 1b) is also morphologically different from that of *Simbirskites* and *Polyptychites*. This suture was erroneously assigned to *A. astieriformis* by Voronets (l. cit.) in the plate explanation and the heading of the description of that species. However, like the previously discussed similarly mislabelled suture of *A. astieriformis*, it is recognizable as that of her *A. astieriptychus* because of structural details discussed in the descriptions proper of these two species. This incomplete suture cannot be oriented definitively on the actual specimen from which it was drawn. However, it has the same angular knicked appearance in the middle as that of *A. obsoletus*. Therefore, it is assumed to be oriented as in this Canadian species. It has three auxiliary lobes according to Voronets (1958, p. 25).

Though Voronets (1958, p. 26) is correct about the external suture line of *Astieriptychites* being more similar to that of *Dichotomites* s.l. (i.e. inclusive of *Prodichotomites* Kemper) than it is to that of *Simbirskites* and *Polyptychites*, the first two sutures are distinguishable as well. The adult suture of *Astieriptychites* has the same number of auxiliary lobes as do the sutures of *Dichotomites* s. str. and *Prodichotomites* and all three sutures belong to the same group of advanced polyptychitinid suture lines. However, the *Prodichotomites* suture line differs in its, as a rule, considerably wider lobes and relatively more narrow saddles. These features are combined with a different orientation of the *Prodichotomites* suture line, which is either markedly to pronouncedly ascendant throughout or combines a slightly ascendant to subradial orientation of its lateral part with a distinctly to pronouncedly retractive orientation of its auxiliary part. Furthermore, the first lateral lobe of *Prodichotomites* is always only insignificantly to moderately (up to one-third) longer and wider than the second lateral lobe (e.g. von Koenen, 1902, Pl. XLVI, fig. 1; Pl. XLVII, fig. 3; this paper, Pl. 15, fig. 2A; Pl. 19, fig. 1B; Figures 44a, 44c, 46a-46c). That of *Astieriptychites* is relatively considerably larger, about twice as long and proportionally wider than the second lateral lobe in all presently known examples of its adult to intermediate external suture lines (Pl. 62, figs. 2A, 2B; Figures 58b, 58c; Voronets, 1958, Pl. 1, fig. 2g). Finally, all elements of the adult to intermediate external sutures of *Prodichotomites* are always considerably more complexly and deeply denticulated than the corresponding elements of equivalent sutures of *Astieriptychites*. So far as is known, all the above morphological distinctions are also valid for the external suture lines of *Dichotomites* s.str. (e.g. von Koenen, 1902, Pl. XLVII, fig. 1; Pl. XLIX, fig. 4; Pl. LIII, fig. 1; Kemper, 1978, Fig. 6). On the whole, the markedly ascendant to subradial orientation of the adult external suture of *Astieriptychites* combined with the presence of three to four auxiliary lobes and other above mentioned morphological distinctions are considered to be more important taxonomically than the distinctions of its adult ribbing habit utilized by Bodylevsky (1960).

It is only because of the association of the predominantly *Olcostephanus*-like ribbing habit of advanced whorls with the fairly wide and step-like umbilicus, the characteristic external suture line, and the absence of characteristic *Siberiptychites*-like sequences of whorl shapes and sculptural stages that the authors grant a full generic status to *Astieriptychites*.

As already mentioned in the discussion of *Bodylevskites* (*see* p. 20, 21 for further details), the recent discovery of that genus in the lower lower Valanginian beds of the Anabar-Khatanga basin provided for the first time a credible ancestor for all endemic polyptychitinids of Northern Siberia, including *Astieriptychites*. The direct derivation of *Astieriptychites* from *Bodylevskites* is indicated first of all by the essentially *Bodylevskites*-like bundling habit and whorl proportions of its early whorls, the presence of *Bodylevskites*-like constrictions on these and more advanced growth stages, and the apparently complete absence of the characteristic *Siberiptychites*-like sequence of whorl shapes and sculptural stages. Furthermore, the ontogenetic development of *Bodylevskites* results in its adult representatives becoming *Astieriptychites*-like in some important respects. For example, its whorl shape gradually becomes sturdier and rounded-trapezoidal in shape while its previously nonbullate primaries are transformed into low bullae on terminal adult whorls. Finally, as pointed out below, the first representatives of *Astieriptychites* are associated with *Bodylevskites* in the regional lower lower Valanginian *Temnoptychites simplicissimus* Subzone of the Anabar-Khatanga Basin.

As it is known now, *Bodylevskites* differs from *Astieriptychites* first of all in the presence of only two auxiliary lobes (instead of three to four) in its early to advanced adult external suture lines. Another important distinction consists in the auxiliary parts of these sutures being pronouncedly retractive (or descendant) according to Klimova's (1978, Figures 4, 5) drawings. Furthermore, the rib bundles of the terminal adult whorls of *Bodylevskites* remain dichotomous to trichotomous (with numerous intercalated supplementary ribs). This contrasts with the predominantly fasciculate bundling habit of advanced whorls of *Astieriptychites*, in spite of the appearance of low, *Astieriptychites*-like bullae on these whorls of *Bodylevskites*. Finally, the adult whorl shape and cross-section of *Bodylevskites* remain much more slender and high than those of equivalent and intermediate whorls of *Astieriptychites*, in spite of the ontogenetic trend toward a more *Astieriptychites*-like appearance of these whorls.

In combination with the restriction of *Bodylevskites* to beds where the first representatives of *Astieriptychites* appear, the similarities and differences in the ontogenetic develoment of these two genera indicate that the generally younger *Astieriptychites* arose very rapidly out of *Bodylevskites* via a predominantly palingenetic (or recapitulational) evolutionary mode.

The inferred additions to the latest ontogeny of *Bodylevskites* that had transformed it into *Astieriptychites* must have paralleled, in part, those that are inferred to have resulted in its transmutation into a closely allied subgenus *Siberiptychites* (see p. 20, 21 for further details). These changes include: 1. The increase of adult auxiliary lobes from two to three or four, the displacement of the five-lobed external suture to the early juvenile growth stages and the loss of the suspensive orientation of the umbilical part of the suture line in the intermediate and adult whorls; 2. Pronounced lowering and thickening of the whorl combined with the development of prominent, forwardly-concave umbilical bullae and the decline of ornament on the mid-flank. These modifications of intermediate and advanced whorls must have been accompanied by a displacement of the *Bodylevskites*-like whorl shape and ornament onto the juvenile and early intermediate ontogenetic stages. All these evolutionary changes parallel those that resulted in its transmutation into *Siberiptychites* s.str. However, other evolutionary modifications, such as the development of a considerably widened, step-like umbilicus, of predominantly fasciculate bundling habit on the advanced whorls, and of the previously discussed distinctive morphological features of the advanced external suture line are peculiar to *Astieriptychites*. Furthermore, the same is true of such "negative" distinctions as the apparently total absence of the complex sequence of whorl shapes and sculptural phases characteristic of the ontogeny of *Siberiptychites* in any presently known *Astieriptychites* species. The presence of these phylogenetically and hence taxonomically important distinctions alongside the parallel and/or convergent evolutionary changes indicates that the genera *Siberiptychites* and *Astieriptychites* are on the whole phylogenetically divergent "daughter genera" of *Bodylevskites* (Figure 11). The transmutation of *Astieriptychites* into the still more distinctive late Valanginian genus *Amundiptychites* (see its description for further details) provides additional support for this conclusion.

Astieriptychites forms part of an important lineage of high Boreal Polyptychitinae, which gave birth repeatedly to morphologically distinctive form groups of ammonites. One of these is represented by ammonites with a *Neocraspedites*-like morphology (e.g. "*Neocraspedites*" *politus* Voronets 1962) while another consists of *Euryptychites*-like forms (N.I. Shulgina, oral communication to E. Kemper, 1982). Its evolution appears to end in the early late Valanginian with gigantic forms, which were described as *Amundiptychites* gen. nov. by Kemper and Jeletzky (1979) and are reviewed below. These terminal evolutionary members of the lineage have apparently lost the otherwise characteristic constrictions. Several specimens of *Astieriptychites* allied to but not conspecific with *A. obsoletus* were recently described and figured from Spitsbergen (i.e. *A. mirus* Yershova 1980). This rather close affinity of geographically remote *Astieriptychites* faunas is rather remarkable and stresses once more their interregional biochronological value.

Stratigraphic relationships and age. According to the latest data available, (e.g. Klimova, 1978, p. 50, 52, 53; 1981, p. 74, 81; Gol'bert et al., 1981, p. 56, 57, Tables 3, 4), the first North Siberian representatives of *Astieriptychites* appear in the lower lower Valanginian *Temnoptychites simplicissimus* Subzone of the regional *Temnoptychites syzranicus* Zone. Klimova (1978, p. 52, 53) points out that they appear in the younger beds of that zone than those containing *Bodylevskites* and the first representatives of *Siberiptychites* (*Siberiptychites*) *stubendorffi*. According to these workers and N.I. Shulgina (personal communication to E. Kemper of 1982), *Astieriptychites* ranges up to the upper limit of the lower Valanginian (i.e. to the top of the provincial *Polyptychites michalskii* Zone) in northern Siberia and other high Boreal basins of Northern Eurasia. Its already mentioned presence in the local equivalents of the *Polyptychites michalskii* Zone of Spitsbergen (Yershova, 1980, p. 70, 71) deserves to be mentioned in this connection. In these basins, *Astieriptychites* must be considered along with *Siberiptychites*, as the most important index fossil of the lower Valanginian.

The earlier records of *Astieriptychites* published by Voronets (1958, 1962) are in a general agreement with the above conclusions about its exclusively early Valanginian age, although the sequence of her "middle Valanginian" (now lower Valanginian) polyptychitinid faunas is somewhat difficult to fit into the presently used regional zones. In the profile of Paks Peninsula the stratigraphically collected material of *A. astieriptychus* and *A. astieriformis* was found in beds situated stratigraphically below those containing *Polyptychites conferticosta* Pavlow but above those containing a variegated *Tollia* fauna (Voronets, 1958, p. 23, 24; 1962, p. 18, Fig. 3). These beds are inferred to correspond to some part of the *Temnoptychites syzranicus* Zone. Elsewhere in the same area (Voronets, 1958, p. 24; Jeletzky's translation from Russian): "a specimen of *Astieriptychites* was found in association with *Polyptychites* cf. *ovatus* Koen., *P.* cf. *rinnei* Koen. and other *Polyptychites* of the upper Valanginian. These beds also include *Euryptychites* and other peculiar forms which may possibly belong to the higher beds of the upper Valanginian". These "*Euryptychites*" are actually representatives of *Pseudoeuryptychites*, which has about the same time range as the subgenus *Siberiptychites* s.str. (see p. 160, 176, 177, 178, 179 for further details). The above listed *Polyptychites* spp. are either closely related to or ?conspecific with the Canadian *Siberiptychites* (nov. subgenus)? n. sp. B that occurs in the Bed 16 of the regional *Siberiptychites* Zone in association with *S.* (*S.*) *stubendorffi*. These Paks Peninsula beds are inferred to represent some part of the *Polyptychites michalskii* Zone of the North Siberian standard.

The above data invalidates the earlier stratigraphic conclusions of Bodylevsky (1957, 1960, p. 173, 174, 175) who had assigned a late Valanginian age to *A. astieriptychus* and *A. tenuiptychus*. This worker (Bodylevsky, 1960, p. 174; Jeletzky's translation from Russian) had expressly designated *A. astieriptychus* as: "An important guide form for the upper Valanginian (zone of *Polyptychites polyptychus*) of northern Siberia." This conclusion conflicted with the data of other Soviet workers that favored a "middle Valanginian" (now lower Valanginian) age of the *Astieriptychites*-bearing beds and caused them to consider this genus to be a longranging, insufficiently understood taxon (e.g. Saks et al., 1963, p. 71, 72, Table 8; Saks and Shulgina, 1974, p. 142). These conclusions were also considered to be valid by Jeletzky (1973, p. 67).

All datable Canadian representatives of *Asteriptychites?* sp. indet. B; see p. 189, 190; Figure 62 for further details) occur in beds which are either contemporary with or slightly older than those containing *Siberiptychites* (*Siberiptychites*) spp. Therefore, they fall well within the by now well established North Siberian time range of *Astieriptychites*.

Astieriptychites obsoletus sp. nov.

Pl. 42, fig. 3; Pl. 49, figs. 2A-2C; Pl. 57, figs. 4A-4K; Pl. 59, fig. 4; Pl. 62, figs. 2A, 2B; Figures 58b, 58c.

Synonymy
1977 *Astieriptychites* Kemper, p. 1.

Type specimen. Specimen GSC Cat. 77110 from the GSC loc. 93865 is the holotype of *Astieriptychites obsoletus* sp. nov. by monotypy.

Other material. None.

Diagnosis. An *Astieriptychites* species which combines the whorl shape and fine, flexuous ribbing habit of *A. astieriformis* Voronets 1958 with a strongly oblique umbilical wall at all known growth stages. The uniquely weak secondary ribs become weakened on the mid-flank beginning with a whorl diameter of about 15 mm and later become almost completely obliterated. The lateral part of the adult external suture line is markedly ascendant, forming an angle of 10 to 15 degrees with the corresponding shell's radius. Its auxiliary part becomes gradually less and less ascendant but does not become radially oriented.

Measurements (in mm).

Shell diameter	Whorl height	Whorl width	Diameter of the umbilicus
Holotype (GSC Cat. 77110) 66.5 (100)	25 (40%)	32.5 (53%)	20.5 (31%)
(half whorl before oral end) 49 (100)	21.5 (44%)	25.5 (52%)	14.0 (35%)

Description.

Whorl shape and proportions. The width of the umbilicus is situated on the border line between moderately involute and moderately evolute (31 to 35 per cent of the shell diameter) and appears to decrease somewhat adorally. The shell is fairly sturdy (height/width ratio 78 to 85 per cent) with the whorl's width exceeding its height at all accessible growth stages. The cross-section is hoof-shaped with the maximum diameter situated at the umbilical shoulder and the but slightly convex flanks contracting almost evenly all the way to the broadly rounded ventral shoulder. The venter is broadly arched and slightly flattened. The umbilical wall is oblique at all visible growth stages; it forms angles of 40 to 45 degrees with the shell's diameter (Pl. 57, figs. 4D, 4F, 4H, 4I). The wall is distinctly convex in the early growth stages up to a whorl diameter of about 25 mm. Later it becomes gradually less so until it becomes approximately straight on the last whorl preserved (Pl. 57, fig. 4D). The umbilical shoulder is almost regularly rounded on the early growth stages until a whorl diameter of about 30 mm (Pl. 57, fig. 4I, 4H, 4F). Thereafter it gradually becomes more and more rounded-angular until it becomes subangular on the last whorl preserved. The umbilicus is markedly step-like at all accessible growth stages.

Sculpture. The earliest whorl visible has an estimated diameter of about 3.5 mm at the oral end (Pl. 49, fig. 2C; Pl. 57, figs. 4E, 4H). Only the upper half of one flank and the venter of the oral half are exposed. These are ornamented by extremely fine, almost striate, very closely spaced supplementary ribs, which are flexuous and bend forward markedly on the flank. They form broad, regularly rounded, forwardly convex arches on the venter (Pl. 57, fig. 4H) where they do not appear either to weaken or to be interrupted. Two very faint and fine, forwardly arched constrictions are discernible on the earliest exposed part of this whorl. So far as it is possible to see, the supplementaries do not branch on its exposed upper flank.

About three-fifths of the next adoral whorl are concealed. The following exposed two-fifths of this whorl (Pl. 49, fig. 2C; Pl. 57, figs. 4E, 4F, 4G, 4I, 4J, 4K), to a diameter of about 18 mm, exhibits a different ornament designated the late juvenile ribbing habit. The lowermost flank is ornamented by fine, fairly closely spaced primary ribs beginning on the rounded umbilical shoulder. Except for the last primary exposed, none are elevated or noticeably thickened. They are markedly forwardly inclined and short; they split up into very fine, closely spaced secondary ribs on the lowermost part of the flank. These low and roundtopped (in the internal mould) secondary ribs are arranged in irregularly alternating trichotomous, less common true polyptychous and rare dichotomous bundles. In some trichotomous bundles all three secondaries split off the primary simultaneously (i.e. are fasciculate) while in others only two secondaries split off at first and the posterior secondary subdivides again higher upflank. This results in a trivirgatitpartitous bundle. In the polyptychous bundles two out of three first order secondaries subdivide in two second order secondaries higher upflank. Some intercalated ribs begin on the midflank between the bundles. In all bundles, regardless of their type, it is the anterior secondary that represents the direct continuation of the primary rib and is firmly attached to it. The other (one or two) secondaries are only indistinctly attached to the primary rib and this connection may be completely lost in some bundles. All first and second order secondaries are markedly sinuous. Their forward inclination gradually increases upflank. All ribs bend forward markedly at the ventral shoulder and form marked, narrowly rounded forward bends on the venter (Pl. 57, figs. 4C, 4E, 4F, 4I, 4J); they are neither weakened nor interrupted on the venter. A solitary, shallow constriction, which is shaped like the adjacent ribs, occurs on the oral part of the exposed segment.

This late juvenile stage is assumed to extend over the greater or lesser part of the entirely concealed early two-thirds of the next adoral whorl. However, its exact extent is uncertain as the following one-third of this whorl (Pl. 49, figs. 2A, 2B; Pl. 57, figs. 4B, 4C, 4D) exhibits a different ornament transitional to the adult ornament described below. This transitional ornament has distinctly thickened and elevated (i.e. slightly bullate) primary ribs which gradually become more strongly elevated and thickened oralward until their uppermost parts occupying the lowermost flank are transformed into oval-shaped, sharptopped bullae at this segment's end (Pl. 57, fig. 4C). This gradual emergence of umbilical bullae in the intermediate growth stage gives rise to the diagnostic feature of the ensuing adult growth stage. These primaries begin in the middle of the umbilical wall leaving its inner half smooth. They cross the outer half of the wall on a subradial to slightly adorally inclined course. Then they bend markedly forward either at or just above the umbilical shoulder and continue on that course over the lower one-fifth to one-quarter of the flank. The primary ribs become gradually thicker and more and more distinctly sharptopped from the point of their inception upflank and reach their maximum strength at the point where they split into secondary ribs. This results in a distinctly comma-like appearance. The secondary ribs of this transitional growth stage do not differ materially from those of the next following adult growth stage (see below).

The bullate adult growth stage extends for about one and a half whorl to the still septate oral end of the specimen. Here the adult bullae (which are more prominent and sharptopped on the shell than on the internal mould) gradually increase in size and prominence adorally to the last preserved part of the shell (Pl. 59, fig. 4) where they are up to 3 mm high, 12 mm long and 6 mm wide. At the same time those parts of the primaries situated on the umbilical wall tend to weaken in comparison with the transitional phase. This results in a locally semismooth appearance of the adult umbilical wall. In spite of the gradual but marked increase in size and prominence of the umbilical bullae, their number per whorl remains about the same throughout the adult stage. They number about 16 per whorl.

The bullate primary ribs split into three to four, and rarely into five, secondary ribs at levels from one-fifth to one-quarter over the flank. All resulting bundles appear to be fasciculate rather than virgatotome or true polyptychous as all secondaries arise at once. However, the connections of secondaries with the bullae are only distinct on the earliest exposed third of a whorl of the adult stage and then only where the shell is preserved. This leaves the exact nature of some bundles and the number of secondaries in them in doubt. Some intercalated secondary ribs arise either low on the flank or in its middle between the bundles.

All secondary ribs are fine, closely spaced and low with the interspaces one and a half to two times wider than the ribs. There is a distinct tendency for the interspaces to become wider toward the oral end of the shell. The ribs are approximately roundtopped whenever preserved as internal moulds but become somewhat sharpened and better delimited in the shell-covered preservation. The secondary ribs are strongly inclined forward across the flank but, unlike the distinctly flexuous ribs of the juvenile growth stage, they are straight to almost straight and do not bend adorally on the ventral shoulder. The broad, adorally decreasing bends of the secondaries on the venter (Pl. 57, figs. 4B, 4D) result from their turning around within the venter proper. Here the secondaries are neither weakened nor interrupted. There are about 80 to 85 secondary ribs per whorl which corresponds to a branching co-efficient of about 5.

A well developed, 2 to 2.5 mm wide, distinctly impressed and delimited, strongly forwardly inclined constriction occurs in the middle of the first adult whorl (Pl. 57, figs. 4A, 4C). This constriction is expressed on both shell and internal mould. Two more closely spaced, 2.5 to 3 mm wide but less impressed and illdelimited constrictions occur about one-quarter of a whorl before the broken oral end of the shell (Pl. 59, fig. 4). These constrictions are strongly inclined forward and form broad forward loops on the venter.

The secondary ribs are only indistinctly attached to the umbilical bullae in the early part of the adult growth stage, as they are distinctly to markedly weakened in a few mm wide zone of the mid-flank just above the bullae. The secondaries become weaker and weaker within this zone until it becomes semismooth to almost smooth near the broken oral end (Pl. 59, fig. 4).

Suture line. The presumably advanced adult suture line of *A. obsoletus* (Pl. 62, figs. 2A, 2B; Figure 58b) is considerably more strongly dissected by auxiliary lobes and lobules than is that of *A. astieriptychus* (see Voronets, 1958, Pl. I, fig. 1b) and *A. astieriformis* (see Voronets, 1958, Pl. I, fig. 2g). Furthermore, it differs from the suture line of *A. astieriptychus* in a considerably greater width of saddles coupled with a considerably lesser width of lobes. The *A. obsoletus* suture is similar to that of *A. astieriformis* (compare Figure 58b with Voronets, 1958, Pl. I, fig. 2g) in this respect but not in the number of auxiliary lobes. There are four auxiliary lobes in the *A. astieriformis* suture line as compared with only three in that of *A. obsoletus*. The figured suture line of *S. astieriptychus* is incomplete and cannot be decifered. However, it is said to have three auxiliary lobes (Voronets, 1958, p. 25, Pl. I, fig. 1b; Voronets, 1962, p. 82). Bodylevsky's (1960, p. 173) statement (Jeletzky's translation from Russian) that it is: "as in *Polyptychites*: lobes and saddles long and narrow, lateral lobes and saddles have almost parallel flanks." leaves out the number of auxiliaries.

The relative sizes of the ventral and lateral lobes of *A. obsoletus* and the width of intervening saddles are similar to those of *A. astieriformis*. However, this part of the *A. obsoletus* suture line differs markedly from that of all North Siberian *Astieriptychites* species in its

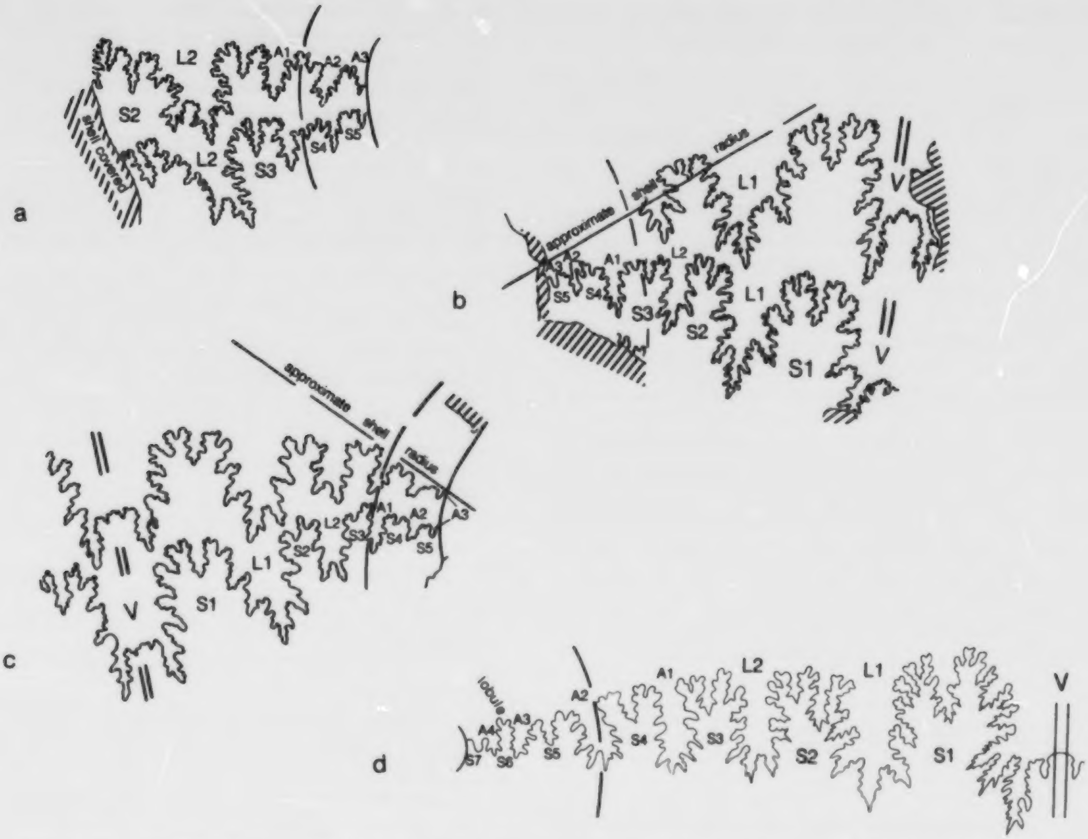


Figure 58. Adult external suture lines of the Sverdrup Basin Polyptychitinae. **a.** *Siberiptychites (Pseudoeuryptychites)* n. sp. indet. A. The otherwise unfigured specimen GSC Cat. 79414 (see p. 179 for further details). Juvenile suture observed at the whorl diameter of about 15 mm, x 4 (approxim.); **b.** *Astieriptychites obsoletus* n.sp. Holotype, GSC Cat. 77110 reproduced in Pl. 57, figs. 4A-4K. Adult (?advanced) suture observed at the shell diameter of about 53 mm, x 1 (approxim.); **c.** *A. obsoletus* n.sp. The same specimen as in Fig. 58b. Early (?earliest) adult suture observed at the shell diameter of about 20 mm, x 2 (approxim.). **d.** *Amundiptychites sverdrupi* Kemper and Jeletzky 1979. Holotype, GSC Cat. 67161 (Pl. 53, fig. 1; Pl. 54, fig. 2; Pl. 66, fig. 2). Adult (advanced) suture observed at the approximate whorl diameter of 81 mm, x 1 (approxim.).

markedly ascendant orientation. Unlike the subradially oriented to slightly suspensive lateral parts of suture lines of *A. astieriptychus* and *A. astieriformis* that of *A. obsoletus* is markedly ascendant and forms an angle of 10 to 15 degrees with the corresponding shell radius (Pl. 62, fig. 2B; Figure 58b). Only the auxiliary part of the suture is subradially oriented, and even here it remains slightly ascendant.

The early (?earliest) adult suture line of *A. obsoletus* observed at a whorl diameter of about 10 mm (Pl. 57, figs. 4F, 4K; Figure 58c) differs from later sutures in the considerably lesser identation of its lobes and saddles. It already has all three auxiliary lobes. The first is situated at the umbilical shoulder, the second occurs in the middle of the umbilical wall, and the third (which is a tiny and simple structure) is at the umbilical seam. This juvenile suture line is just as markedly ascendant in its lateral part as is the adult suture line. Only its auxiliary part becomes slightly ascendant to subradial.

Stratigraphic relationships and age. The single specimen of *Astieriptychites obsoletus* was found loose on the surface of the very poorly exposed upper member of the Mould Bay Formation on the northern part of Mackenzie King Island, approx. Lat. 77°54'N.; Long. 111°09'W. (see Kemper, 1977, p. 1 for further details). Elsewhere on the island, this upper member has yielded a *Buchia* cf. *keyserlingi* (Lahusen) fauna locally associated with *B.* cf. *inflata* (Toula)(Tozer and Thorsteinsson, 1964, p. 146). This *Buchia* fauna can only be assigned a general early Valanginian age. However, because of the association of *Astieriptychites* sp. indet. A and *Astieriptychites*? sp. indet. B with *Siberiptychites stubendorffi* in Reptile Creek on Ellesmere Island (see p. 189) *Astieriptychites obsoletus* is assumed tentatively to be derived from some part of the regional *Siberiptychites* ex gr. *stubendorffi* Beds.

Affinities and differences. The morphological distinctions of *A. obsoletus* from previously described *Astieriptychites* species have been discussed above. Another close ally is the scantily and incompletely described and poorly figured "*Neocraspedites*" *mirus* Yershova 1980 from Spitsbergen. This species is not a true *Neocraspedites* as interpreted in this paper, nor could it be a member of any other European Polyptychitinae genus (except for *Bodylevskites*) because of the presence of constrictions (Yershova, 1980, p. 75). It appears to be an *Astieriptychites* similar to *A. obsoletus* but with a considerably more slender, rounded-rectangular, subparallel-flanked adult whorl section (Yershova, 1980, p. 75, Pl. VII, figs. 1b, 2b, 3b, 4b; Pl. VIII, figs. 2b, 4b, 5b). Furthermore, its supplementary ribs become first strongly weakened and then (by 20-35 mm shell diameter), completely lost on the lower flank much earlier than in *A. obsoletus*. Finally, "*N.*" *mirus* is a considerably or ?much smaller form than *A. obsoletus*; according to Yershova (1980, p. 75, Pl. VII, fig. 1) its adult representatives with most of their living chamber preserved have shell diameters in the order of 60-70 mm. The Canadian species is, in contrast, still fully septate at a maximum preserved diameter of about 90 mm.

Astieriptychites sp. indet. A

Pl. 55, fig. 1

Material. Three fragmentary, almost completely squashed intermediate whorls from GSC loc. 91354 (=Ke 74/2/2), two similarly preserved fragments from GSC loc. 91374 (=Ke 74/6/0) and two similarly preserved fragments from GSC loc. 91376 (=Ke 74/6/0 but on the float).

Description. All the above-mentioned specimens are referable to *Astieriptychites* because the secondary ribs of their intermediate whorls branch in bundles of three and four directly from the comma-like, strongly elevated, sharptopped umbilical bullae. Some intercalated ribs occur between the bundles but the polyptychitinid branching of secondaries higher upflank was not observed in any of the specimens. Their strongly elevated, sharptopped secondary ribs are firmly attached to the bullae and do not weaken on the mid-flank (e.g. GSC Cat. 77123; Pl. 55, figs. 1A, 1B). The secondary ribs cross the venter without any weakening let alone interruption; they appear to be inclined forward on the upper flank and to form feeble forward loops on the venter but none of the specimens is well enough preserved to be certain.

The original shape and proportions of the whorl are completely destroyed on all specimens, and no suture line is exposed.

Remarks. The ribbing habit of *A.* sp. indet. A is similar to that of *A. astieriptychus*, but the Canadian forms are left in open nomenclature as the suture line and the shape and proportions of the whorl and umbilicus remain unknown. Compared with *A. obsoletus*, *A.* sp. indet. A has much coarser and more elevated, sharptopped secondary ribs, which do not weaken on the mid-flank in any of the observable, intermediate growth stages.

From *Astieriptychites tenuiptychus* and *A. astieriformis A.* sp. indet. A differs in a considerably coarser and sparser ribbing habit.

Stratigraphic relationships and age. All 7 specimens were found in the faulted Reptile Creek section on Ellesmere Island. The Lower Cretaceous part of this section has yielded otherwise only a *Temnoptychites* (*Costamenjaites*) *troelseni* Jeletzky fauna of a presumably older, possibly basal Valanginian age (Jeletzky, 1979, p. 56-58, Fig. 8). However, the stratigraphic relationships of these two faunas remain uncertain because they are inferred to be separated by a fault (Tozer and Thorsteinsson in Douglas et al., 1970, p. 581, 582, Fig. X-12). The only other clue to the age of the *A.* sp. indet. A fauna is its association with *Siberiptychites* (*Siberiptychites*) *stubendorffi* (Pavlow) (Pl. 42, fig. 4) at fossil locality GSC 91354 (=Ke 74/2/2). The latter specimen was found in the float (personal communication, E. Kemper, August 1974). However, as the locality is assumed to be situated only about 60 m stratigraphically below the base of the Isachsen Formation (personal communication, E. Kemper, August 1974), *S.* (*S.*) *stubendorffi* can hardly be much younger than *A.* sp. indet. A. The two are assumed to be approximately contemporary for the purpose of this paper (Figure 62) so the *A.* sp. indet. A fauna is assigned tentatively to some part of the regional *Siberiptychites* (*Siberiptychites*) ex gr. *stubendorffi* Beds. This confirms the presence of a prolonged hiatus between the Deer Bay and the Isachsen Formations in this area of the Sverdrup Basin postulated by Tozer and Thorsteinsson (in Douglas et al., 1970, p. 581, 582, Fig. 8-12) and confirmed by subsequent work.

Astieriptychites? sp. indet. B

Pl. 42, figs. 5A, 5B.

Material. Only completely flattened, fragmentary specimen GSC Cat. 77112 from GSC loc. 91376 (=Ke 74/6/2, float).

Description. The solitary specimen differs from the associated *A.* sp. indet. A in its much finer and more closely spaced ribbing habit, which is comparable to that of *Astieriptychites tenuiptychus*, *A. astieriformis* and *A. obsoletus*. Furthermore, it exhibits exceptionally fine and closely spaced comma-like umbilical bullae which number between 20 and 22 on the side of the whorl shown in Pl. 42, fig. 5A. However, the mode of bundling of the secondaries is not clearly visible on any part of the whorl. The secondary ribs are strongly weakened on the midflank of the adoral half of the preserved whorl (Pl. 42, fig. 5A).

Remarks. Because, in particular, of the weakening of secondary ribs on the midflank, the specimen may be a poorly preserved representative of *A. obsoletus*. However, the shape and proportions of the whorl, width of umbilicus and suture line remain unknown. Furthermore, its reference to *Astieriptychites* is somewhat uncertain as the mode of bundling of the secondary ribs is nowhere clearly visible. Hence it is designated as *A.*? sp. indet. B.

Stratigraphic relationships and age. The specimen was found in the Reptile Creek section of Deer Bay Formation on Ellesmere Island at GSC loc. 91376. Therefore, its stratigraphic position and age are believed to be approximately the same as for *A.* sp. indet. A collected at this locality. However, the fossils of locality 91376 were collected on the float and according to E. Kemper (who collected them) they may have dropped down: they could accordingly be from beds which are up to 10 m higher in the profile.

Genus *Amundiptychites* Kemper and Jeletzky 1979

Synonymy
1979 *Amundiptychites* Kemper and Jeletzky, p. 3, 4.

Origin of name. From the occurrence of the originally described material (Kemper and Jeletzky 1979) on Amund Ringnes Island, N.W.T.

Type species. Amundiptychites sverdrupi Kemper and Jeletzky, 1979.

Diagnosis. Large (adult shell diameter up to 250 mm or ?more) Polyptychitinae which have broad and low, subcircular whorl cross-section and an evolute umbilicus in early (sometimes earliest only) growth stages but tend to develop rounded-trapezoidal considerably higher whorls with a narrowly arched venter and completely funnel-like umbilicus, in subsequent (including partly adult) growth stages. Ribs and umbilical nodes are fine and closely spaced on the early and intermediate whorls. Ribbing habit is mostly polyptychous but at least some rib bundles on the intermediate growth stages are fasciculate (i.e. *Olcostephanus-* or *Astieriptychites*-like). Adult sculpture (i.e. that of adult last and penultimate whorls) consists of coarse, widely spaced ribs arranged in polyptychous bundles and large and prominent, conical bullae. No constrictions were noted in any investigated growth stage. The adult external line has from 3 to 5 (mostly) auxiliary lobes.

Remarks. The morphological features listed in the diagnosis of *Amundiptychites* attest to its highly peculiar, truly remarkable character. Similar combinations of morphological features have not been observed in Polyptychitinae of other regions, except in the presumably ancestral *Astieriptychites*. Extraordinary and particularly remarkable for the genus is the sequence of morphologically very different ontogenetic stages, as comprehensively discussed below in the description of *A. sverdrupi*. As is evident already from the description of *Polyptychites canadensis* and *Siberiptychites*, major ontogenetic changes are prominent in some other evolutionary lineages of Polyptychitinae too. These changes always complicate a definitive identification of species whenever the material is poorly preserved. However, except in *Siberiptychites*, none of these changes are as far reaching as those occurring in *Amundiptychites*.

From *Polyptychites*, *Amundiptychites* differs in the very fine and closely spaced character of ribs on the early and intermediate whorls and a funnel-like umbilicus of later growth stages. This ribbing habit is combined with equally delicate, closely spaced and pronouncedly comma-like umbilical bullae. Furthermore, the early to late adult external suture lines of *Amundiptychites* have three to five auxiliary lobes and so are advanced rather than typically polyptychitinid in their character (see in the introductory chapter for further details). However, this suture line is rather variable within the genus in a fashion which attests its polyptychitinid affinities. In the evidently still primitive *Amundiptychites fasciatus* n.sp., the adult suture line has only three auxiliary lobes as in *Astieriptychites*. In the morphologically more advanced *A. sverdrupi* Kemper and Jeletzky and *A. thorsteinssoni* n.sp., however, it has 4 to 5 auxiliaries. The predominantly polyptychous rib bundles of the early and intermediate whorls of *Amundiptychites* are either interspersed with fasciculate *Olcostephanus-* or *Astieriptychites*-like rib bundles or are replaced by the latter on at least some intermediate whorls. From *Siberiptychites* and *Astieriptychites*, *Amundiptychites* differs in the above features and in an apparently complete absence of constrictions, which are characteristic or these two taxa. *Astieriptychites* differs also in the apparently complete absence of coarsely ribbed, tubular-shaped juvenile whorls characteristic of some *Amundiptychites*.

Because of the above mentioned features, the early and intermediate whorls of *Amundiptychites* resemble the adult whorls of *Astieriptychites*. However, already the different timing of the appearance of these features combined with an apparently complete absence of constrictions in *Amundiptychites* attest to its generic independence. Furthermore, *Amundiptychites* differs from *Astieriptychites* in an entirely different sculpture of its adult penultimate and last whorls. There the *Astieriptychites*-like sculpture is replaced by one consisting of very large and prominent, oval, rather sparse bullae and coarse, widely spaced secondary ribs forming polyptychous bundles. Another distinctive feature of *Amundiptychites* is an unusually early weakening of the sculpture on adumbilical parts of the flanks, which begins already at a shell diameter of 70 to 90 mm. Although weakening occurs commonly at more advanced growth stages in other polyptychitinid genera occurring in the Sverdrup Basin, a comparably early weakening was observed only in *Astieriptychites obsoletus*, *A. mirus* and *Astieriptychites*? sp. indet. B. Yet another characteristic feature of *Amundiptychites* is the more or less prolonged retention (it ends at shell diameters ranging from about 15 mm to about 70 mm) of a widely umbilicate juvenile growth stage with an approximately subcircular (i.e. tubular) whorl section. The sculpture of this juvenile stage is, generally, similar to that of the intermediate whorls but may be appreciably coarser in some forms (e.g. *A. sverdrupi*). The infrageneric variation of this juvenile growth stage permits the recognition of two groups of species in *Amundiptychites*.

1. *A. sverdrupi* is characterized by the great duration (to a shell diameter of about 70 mm) of the juvenile growth stage, which is marked by the tubular whorl section and coarser sculpture than in the following intermediate growth stage; and

2. All other species (e.g. *A. thorsteinssoni* n.sp. described below), in which this juvenile growth stage is relatively shortened (it is restricted to the earliest studied growth stages with a shell diameter less than 30 mm) and does not seem to be more coarsely sculptured than the intermediate growth stages.

The width and shape of the umbilicus and the whorl shape of this juvenile growth stage resemble those of adult *Astieriptychites* (see below). This juvenile stage is followed by a stage characterized by relatively slender hoof- or wedge-shaped to rounded-trapezoidal, mostly narrow-ventered whorl section and delicate sculpture. This growth stage resembles that of the somewhat later *Prodichotomites* species on the one hand and that of the contemporary representatives of the *Polyptychites* ex gr. *canadensis* on the other. These similarities appear to be homoeomorphic in character as the sculpture of the preceding juvenile and the following adult whorls of *Amundiptychites* differs strongly from that of the equivalent whorls of the other two taxa.

Kemper and Jeletzky (1979, p. 4, Figure 8) suggested that *Amundiptychites* is more likely a descendant of the somewhat older *Astieriptychites* than an ally of either the late, laterally compressed *Polyptychites* or the early *Prodichotomites*. This conclusion is adhered to in this paper. *Amundiptychites* does resemble *Astieriptychites* closely in several ways. For example, the strong resemblance of the juvenile and intermediate growth stages of *Amundiptychites* to the adult growth stages of *Astieriptychites* combined with the much larger adult size of the former genus is definitely suggestive of the former having evolved from the latter by palingenesis. The apparently complete absence of constrictions in all presently known Canadian representatives of *Amundiptychites* does not contradict this conclusion either as transitional forms between them and *Astieriptychites* appear to be present elsewhere. For example, "*Neocraspedites*" *gratissimus* Yershova 1980, which is morphologically similar to *A. thorsteinssoni* and is assigned tentatively to *Amundiptychites* in this paper, does exhibit constrictions in its early growth stages (Yershova, 1980, p. 74; Pl. V, fig. 2b). This Spitsbergen species appears to be late early Valanginian in age because of its reported occurrence in the "*Polyptychites ramulicosta* Zone" which is, in fact, based on misidentified representatives of *Siberiptychites* (*Siberiptychites*) *stubendorffi* (i.e. Yershova, 1980, Pl. VI, fig. 2a and p. 141, 151 of this paper). Therefore, *Amundiptychites*? *gratissimus* is presumably a connecting link between the more sturdy *Astieriptychites* forms occurring in Spitsbergen (e.g. *A. mirus* Yershova 1980) and the slender, late Valanginian representatives of *Amundiptychites* (e.g. *A. thorsteinssoni*) that appear to be totally devoid of constrictions.

Amundiptychites sverdrupi Kemper and Jeletzky 1979

Pl. 48, fig. 1A, 1B; Pl. 49, fig. 1; Pl. 53, figs. 1, 2; Pl. 54, figs. 2A, 2B; Pl. 66, fig. 2; Figures 58d, 59a.

Synonymy

1979 *Amundiptychites sverdrupi* Kemper and Jeletzky, p. 4, 5; Pl. 3, fig. 1; Pl. 4, fig. 1a, 1b; Figure 3.

Origin of name. For Otto Sverdrup, an outstanding explorer of the Canadian Arctic Archipelago.

Holotype. Specimen GSC Cat. 61761 originally figured by Kemper and Jeletzky (1979, Pl. 4, fig. 1a, 1b; Pl. 3, fig. 1; Figure 3) and refigured here in Pl. 53, fig. 1; Pl. 54, fig. 2; Pl. 66, fig. 2; Figure 58d.

Material. Four specimens from GSC loc. 93753, 91303, 61765, and 85059.

Locus typicus. Amund Ringnes Island, N.W.T.; NW part of the island; Lat. 78°38'20"N; Long. 97°56'.

Stratum typicum. Upper Deer Bay Formation, fossiliferous beds 8-9 of Kemper (1977, Fig. 3) designated as Tschekanovskii Beds by Kemper and Jeletzky (1979, p. 13, Figure 9). Apparently uppermost lower Valanginian (i.e. the uppermost part of *Polyptychites michalskii* Zone; see Figure 62).

Diagnosis. Large-sized *Amundiptychites* which features a prolonged juvenile growth stage (up to the shell diameter of about 70 mm) characterized by a subcircular whorl section and relatively coarse ribbing. The intermediate and adult whorls are hoof-like to rounded-trapezoidal and invariably wider than high (height/width ratio of 80 to 90 per cent). The early to late adult external suture line has four to five auxiliary lobes.

Measurements in mm.

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
GSC Cat. 61761 (Holotype)	194	49 (25)	64 (33)	81 (42)	71	93

Description. The last preserved segment of the last whorl of the holotype is a (nonseptate) living chamber. Its sculpture indicates that it is actually a remnant of the adult last whorl, the adoral half of which is still missing. The complete size of the shell can therefore only be estimated at approximately 240 mm.

The earliest four or ?five whorls are not exposed and the juvenile growth stage is first visible at the shell diameter of about 40 mm in the fifth? before last whorl of GSC Cat. 61765 (Pl. 49, fig. 1A, 1B) where the wh 2 : wth 2 ratio comprises 21:22. This nearly equidimentional and subcircular cross-section is distinctly egg-shaped because of the adventrally increasing contraction of the upper flanks and a somewhat narrowly arched venter. The umbilicus is very evolute (about 50 per cent) and markedly step-like, with a markedly convex umbilical wall inclined at about 60 degrees to the whorl's plane of symmetry. This evolute and tubular whorl shape persists through the next one and a half whorls of GSC Cat. 61765 to the shell diameter of about 70 mm (Pl. 49, fig. 1B);

it becomes somewhat more distinctly egg-shaped adorally. The advanced phase of this juvenile growth stage is represented by the earliest exposed whorl segment of the holotype (i.e. its fourth before last whorl; see Pl. 54, fig. 2A, 2B) with the shell diameter of about 60 mm. This phase, which also extends to the shell diameter of about 70 mm, differs from the late phase of GSC Cat. 61765 in a subcircular, regularly arched cross-section of the ventral rounding (Pl. 54, fig. 2A). Furthermore, it is somewhat more lower-whorled with the wh 2 : wth 2 ratio of 20:25. The juvenile, tubular growth stage must end considerably earlier (i.e. before the shell diameter of 40 mm) in the GSC Cat. 77122 (Pl. 53, fig. 2D, 2E) than in the other two examples as the fragment of this earliest preserved whorl, which is approximately equivalent to the innermost exposed whorl of GSC Cat. 61765, is already distinctly hoof-shaped and adventrally narrowed throughout its extent.

The whorl shape changes rapidly from approximately subcircular to a hoof-like between the fourth before last and the third before last whorls of the holotype (Pl. 54, fig. 2A), though it remains approximately equidimentional (i.e. the wh 2 : wth 2 ratio is 38:38 at the shell diameter of about 90 mm). The values given in the table of measurements have been measured at the still later growth stages. The same change of the whorl shape occurs also in GSC Cat. 61765 (Pl. 48, fig. 1B). This intermediate, hoof-like stage is retained through the third before last and the early part of the adult penultimate whorls while gradually becoming considerably sturdier and lower whorled (e.g. its height/width ratio is about 82 per cent at the shell diameter of about 165 mm). Simultaneously the somewhat narrowly rounded venter and the distinctly convex flanks of the third before last whorl gradually become respectively broadly rounded and almost straight on the adult penultimate whorl. Finally, the cross-section of the adult last whorl becomes broadly rounded-trapezoidal with virtually straight, rapidly adventrally converging flanks separated from the broad, slightly convex venter by very broadly rounded umbilical shoulders (Pl. 54, fig. 2A). This adult growth stage remains somewhat wider than high with the height/width ratio of about 90 per cent at the shell diameter of about 215 mm.

The umbilical shoulder of the last three whorls gradually becomes more and more narrowly rounded; it merges more and more rapidly into the progressively less and less convex umbilical wall, which is consistently inclined at about 60 degrees in relation to the shell's plane of symmetry, and becomes appreciably higher as the width of the whorl increases. The very evolute and shallow umbilicus of the juvenile growth stage changes accordingly into a deep, funnel-like, moderately involute (it is only about 25 per cent in the last three whorls) structure (compare Pl. 54, fig. 2B with Pl. 54, fig. 2A).

The bullae are prominent throughout the known growth stages and dominate the sculpture of the last two whorls (Pl. 49, fig. 1A; Pl. 53, fig. 1; Pl. 66, fig. 2). Until the shell diameter of about 90 mm they are essentially radially oriented, only slightly comma-like bent, bullate primaries of a varying relief which appear in the middle third of the umbilical wall and subdivide on the lowermost flank (Pl. 48, fig. 1A; Pl. 49, fig. 1A; Pl. 53, fig. 2A, 2B; Pl. 54, fig. 2B). 17 bullae were counted on the earliest exposed (i.e. fourth before last) whorl of the holotype ending at the shell diameter of about 60 mm (Pl. 54, fig. 2B). In the later, intermediate growth stage the bullate primaries become strengthened and clearly comma-like bent forward on the umbilical wall. Then on the adult penultimate and the adult last whorls they are transformed into much more prominent, approximately conical bullae. The distance separating the individual bullae increases concurrently which results in the estimated presence of only 10 to 12 large, conical bullae on the adult last whorl (Pl. 53, fig. 1; Pl. 54, fig. 2A, Pl. 66, fig. 2).

The earliest visible ribbing habit, which occurs at the shell diameter of about 40 to 60 mm (Pl. 49, fig. 1A, 1B; Pl. 54, fig. 2A, 2B), is dense, moderately strong and irregular; these polyptychous rib bundles mostly include two well formed secondary ribs. A tertiary, single or bifurcating rib intercalated between these secondaries splits off the posterior secondary and another longer, single to bifurcating tertiary rib may split off the anterior secondary. These branching points of the two secondaries are situated at about the same level somewhat above the flank's middle and they both bifurcate once more near or at the ventral shoulder. This produces a total of six to eight supplementary ribs which cross the venter without any weakening and either subtransversally (Pl. 54, fig. 2A) or with a marked forward bend (Pl. 49, fig. 1B). Similar but considerably more prominent and more sparce ornament persists through the preserved oral half-whorl of the next older (third before the last) whorl of GSC Cat. 61765 (Pl. 48, fig. 1A, 1B) to the shell diameter of about 80 mm. Then the ornament becomes rapidly strongly weakened and indistinct on the flank. In contrast, the ornament of the equivalent, third before last whorl of the holotype (Pl. 53, fig. 1; Pl. 66, fig. 2) remains about as fine and dense as on the preceding whorl of GSC Cat. 61765 to the shell diameter of about 80 mm. Furthermore, this ornament is considerably less prominent and rather illdefined (particularly on the semismooth flank) in comparison with that of the equivalent, third before last whorl of GSC Cat. 61765 which may be influenced by its appreciable weathering. The ornament of the similarly sized and presumably equivalent older whorl fragment of GSC Cat. 77122 (Pl. 53, fig. 2A-2C) is about as fine and dense as that of the holotype. However, its supplementary ribs are considerably better defined and distinctly flexuous on the flank and bend distinctly forward on the venter.

The bundling habit mostly cannot be observed clearly after its initial weakening on the preserved parts of the adult penultimate and the adult last whorls of GSC Cat. 61761 and 61765. These flanks are mostly semismooth to smooth between the large, conical umbilical bullae and the prominent adventralmost parts of the supplementary ribs (e.g. Pl. 49, fig. 1A). However, the somewhat better defined rib bundles on the adult living chamber of the holotype (Pl. 53, fig. 1) have two to three secondary ribs per bulla which bifurcate at different levels on the flank. All ribs of these apparent polyptychous bundles are coarse and sparce but low and not accentuated.

Well preserved and complete external suture lines are exposed on the adult penultimate whorl of the holotype at an approximate whorl diameter of about 81 mm (Figure 58d). This advanced adult suture has four normally developed auxiliary lobes. Another small and simple, roundtipped lobe-like structure, which may be either a lobule of the relatively widened seventh lateral saddle (most likely) or the underdeveloped fifth auxiliary lobe, occurs between the fourth auxiliary and the umbilical seam. The slender and subparallel-flanked lobes gradually and more or less evenly decrease in size all the way to the umbilical seam. They also become gradually less and less complexly denticulated in this direction. The second order lobules dissecting the long first order lobules are most common and deepest in the ventral lobe and almost restricted to this lobe and the first and second lateral lobes. The auxiliary lobes are almost exclusively simply and shallowly denticulated. All lobes are symmetrically to asymmetrically trifid.

The lateral saddles are from 1 1/2 to 2 times wider than the preceding lobes, with the exception of the fifth lateral saddle which is about 2 1/2 times wider than the second auxiliary lobe, and the sixth lateral saddle which is slightly more narrow than the third auxiliary. The first and second lateral lobes and the first auxiliary lobe are situated on the flank with the second auxiliary lobe straddling the umbilical shoulder. This, and the positioning of the remaining two auxiliairies on the umbilical wall, results in a rather crowded appearance of the umbilical part of the suture (Figure 58d).

The lateral part of the suture line is distinctly ascendant to the third lateral saddle where it rapidly turns around into a subradial orientation which is then maintained to the umbilical seam.

The external suture line of the GSC Cat. 77122 (Pl. 54, figs. 2A, 2B; Figure 59a) only differs from that of the holotype (Figure 58d) in the presence of a fairly large, distinctly notched fifth auxiliary lobe which is situated almost at the umbilical seam.

Affinities and differences. The relatively greater duration of the tubular, very evolute juvenile growth stage distinguishes *A. sverdrupi* from all other *Amundiptychites*. Compared with the discoidal *A. thorsteinssoni*, it also has a considerably more sturdy and wider (always wider than high) intermediate and adult whorl cross-sections. Compared with *A. fasciatus*, the species has more slender whorls and a less acutely arched cross-section at equivalent growth stages, a shallower umbilicus, and more auxiliary lobes. From *A.* aff. *sverdrupi* it differs in a less prominent sculpture in equivalent growth stages, considerably to much less prominent forward bends of supplementary ribs on the venter, and a feeblier development or a complete absence of the flexuosity of supplementaries on the flank. However, there is a great deal of variation in all these features in the studied material of *A. sverdrupi* (see in its description). In particular, the two fragments of GSC Cat. 77122 have considerably more prominent supplementary ribs which are markedly and narrowly forward bent on the venter. Furthermore, its supplementaries are distinctly flexuous on the flanks and its tubular, very evolute juvenile growth stage must have ended considerably earlier than that of GSC Cat. 61761 and 61765. The paratype GSC Cat. 77122 is morphologically transitional to *A.* aff. *sverdrupi* in all these features. Furthermore, the two were found together at the GSC loc. 85059. Therefore, it is not impossible that *A.* aff. *sverdrupi* is an extreme morphological variant of *A. sverdrupi*.

Amundiptychites sverdrupi is an especially interesting species which offers an excellent example of the sequence of very different morphological growth stages that occur in the high Boreal polyptychitinids. In this instance the growth stages are so different morphologically that one would doubt their belonging together if the species would have been represented by fragments alone. It only became possible to identify such fragments of *A. sverdrupi* (i.e. the paratypes GSC Cat. 61765 and 77122) as conspecific after their forming parts of the same shell and the correct ontogenetic sequence became known through the study of the almost complete holotype.

Stratigraphic relationships and age. The species appears to be restricted to fossiliferous beds 8-9 of Kemper (1977, Fig. 3) and so is diagnostic of the Tschekanovskii Beds (Kemper and Jeletzky, 1979, p. 13, Figure 9) which are assigned to the uppermost lower Valanginian (Figure 62).

Amundiptychites aff. *A. sverdrupi* n. sp.

Pl. 47, figs. 1A-1D.

1979 *Amundiptychites* aff. *A. sverdrupi* Kemper and Jeletzky, p. 22, Pl. 3, fig. 2.

Material. Fragment of shell from GSC loc. 85059, GSC Cat. 61762.

Locus typicus. Northwestern part of Amund Ringnes Island, District of Franklin, N.W.T. No further details available.

Measurements in mm.

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
GSC Cat. No. 61762*	66	15(23)	21(32)	31(47)	20	29

*All measurements approximate only as the fragment is appreciably deformed and is somewhat sturdier than it appears to be.

Description. The fragmentary specimen is septate to the end and is presumed to represent the early whorls only because of its pronounced sculpture which is not weakened at all on the lower flank of the last halfwhorl. The character of the intermediate and adult whorls is therefore unknown.

The last preserved whorl appears to be narrow and high in cross-section. However, it may have been appreciably, and even considerably, sturdier and lower originally than it is now as the fragment is deformed and fractured (Pl. 47, fig. 1D). If so, the fragment may have

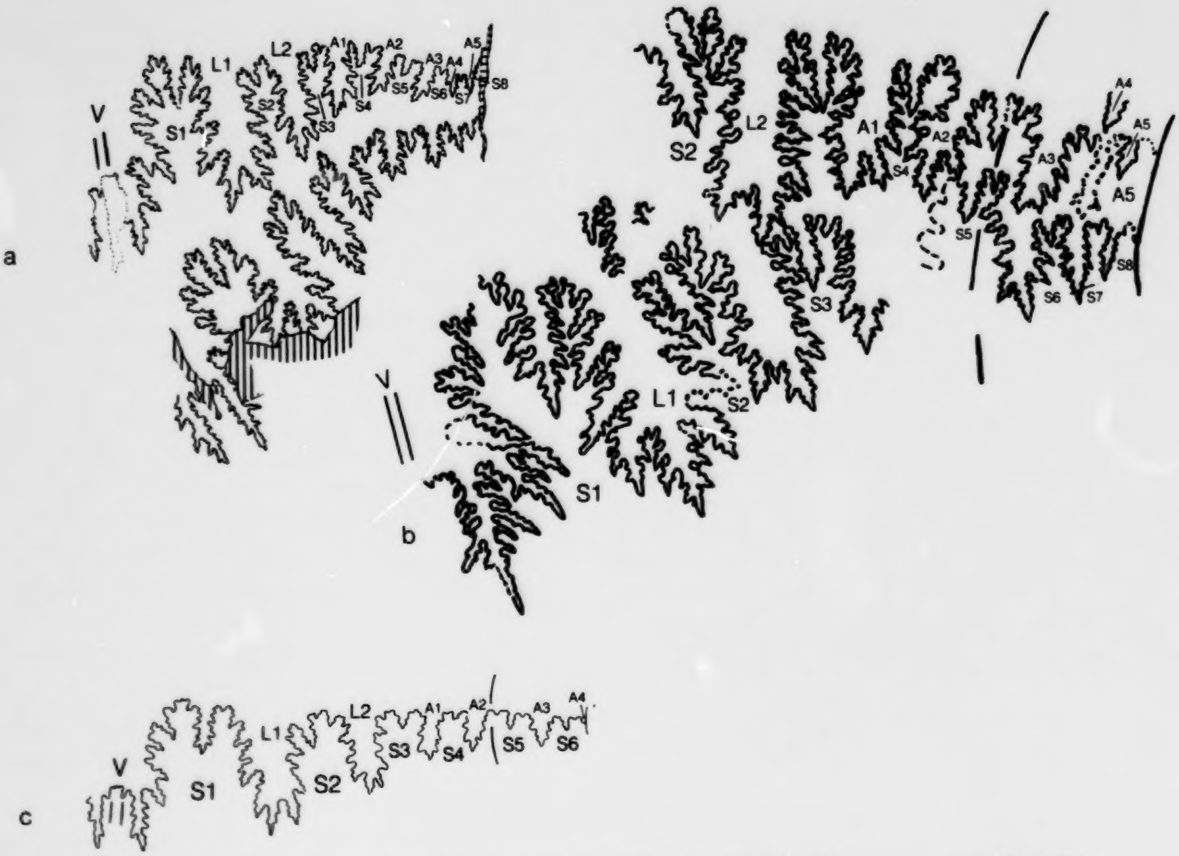


Figure 59. Adult and juvenile external suture lines of *Amundiptychites*. **a.** *A. sverdrupi* Kemper & Jeletzky 1979. Second paratype, GSC Cat. 77122 (Pl. 53, fig. 2). Early adult sutures observed at the whorl diameter of about 36.5 mm; **b.** *A. thorsteinssoni* n. sp. Holotype, GSC Cat. 77135 (Pl. 61, fig. 2, etc.). Advanced adult sutures observed at the oral end of the oralmost preserved whorl (Pl. 61, figs. 2A, 2C) at the approximate whorl diameter of 95 mm; **c.** *A. thorsteinssoni* n. sp. Paratype, GSC Cat. 77125 (Pl. 56, fig. 1) late juvenile suture observed at the whorl diameter of about 33 mm. All figures x 1 (approximately).

resembled *A. sverdrupi* more closely than *A. thorsteinssoni* as was already proposed by Kemper and Jeletzky, (1979, p. 22, Pl. 3, fig. 2). The flanks of the last and penultimate whorls preserved are only slightly convex and merge into a narrowly arched ventral rounding. Their umbilical shoulder is broadly rounded and the distinctly convex umbilical wall is relatively gently inclined (Pl. 47, fig. 1D). The involution is very great as it reaches 85 per cent and the succeeding whorl reaches to the rounding of the umbilical shoulder of the preceding one. This and the oblique orientation of the convex umbilical wall result in a pronouncedly funnel-like shape of the rather narrow umbilicus.

The shape and proportions of cross-sections of the four preserved inner whorls enclosed by the penultimate whorl (Pl. 47, fig. 1D) are similar to the equivalent whorls of the paratype of *A. sverdrupi* (Pl. 49, fig. 1 and the table of measurements). They are approximately tubular in cross-section to a shell diameter of about 30 mm and then become rounded-trapezoidal at the beginning of the preserved half whorl of the penultimate whorl (Pl. 47, fig. 1D).

The fragment is almost entirely shell-covered, which precluded the study of its external suture line. Only small fragments of the latter were observed locally.

The sculpture has an unusual appearance. On the early whorls there are slender, strongly elevated and sharptopped principal ribs rather than true bullae. They extend to the middle of the umbilical wall and are approximately radially oriented. On the last preserved whorl they are transformed into typical, slender and sharp-topped bullae which peter out on the rounded surface of the umbilical shoulder. These bullae are forwardly convex (Pl. 47, figs. 1A, 1B) and subdivide on the lowermost flank.

The ribbing is very dense, fine and strongly bent forward on the upper flank and the ventral shoulder. All ribs form pronounced but broad forwardly-convex arches on the venter, which they cross without any weakening

(Pl. 47, fig. 1C). Most of the rib bundles are distinctly fasciculate in the proximity of the umbilical shoulder on the early part of the last preserved half whorl. However, some of them bifurcate again higher upflank producing true polyptychous or tridichotomous bundles. Together with locally present intercalated secondaries, there are 6 to 7 supplementary ribs per bulla on this part of the whorl (Pl. 47, figs. 1A, 1B). Farther adorally the bundling habit changes to a predominantly tridichotomous mode (e.g. Pl. 47, fig. 1A, 1B) with each of the three secondaries generally bifurcating at about the same level at or somewhat below the flank's middle. Some of the secondaries (usually either the anterior or the posterior or both) are only indistinctly connected to their bulla and rare intercalated, single or bifurcating ribs may occur between the bundles. Finally, rare secondaries may subdivide twice forming a trivirgatitid element.

Affinities and differences. *A*. aff. *A. sverdrupi* can only be compared with the equivalent growth stages of other *Amundiptychites* species and it is judged to be most similar to *A. sverdrupi* and *A. thorsteinssoni* (in that order). From these it differs especially in the delicate but high ribs and in an early appearance of true fasciculate rib bundles with 6 to 7 supplementary ribs.

As already noted (p. 193), the strong forward arching of ribs on the venter is not restricted to *A*. aff. *sverdrupi*. The ribs of the paratypes of *A. sverdrupi* shown in Pl. 48, fig. 1B and Pl. 53, figs. 2A-2E are similarly strongly arched forward on the equivalent and earlier whorls. Only those of the holotype cross the venter in an almost transversal direction. Furthermore, the cross-sections of the early whorls of the GSC Cat. 77122 do not differ much, if at all, from those of *A*. aff. *sverdrupi*. Finally, the high and sharp appearance of ribs of *A*. aff. *sverdrupi* may be a matter of preservation (shell covered specimen!) only. The apparently distinctive narrow umbilicus and the apparently slender whorls, which occur otherwise only on the small specimen of *A. thorsteinssoni* (Pl. 56, fig. 1A-1D) may be caused by a postmortal deformation. If so, the inner whorls could have been much wider and lower originally than they are now. On the whole, there is little doubt that *A*. aff. *sverdrupi* is very closely allied to *A. sverdrupi* and could be an extreme morphological variant of that species.

The superficial resemblance (primarily in the forward arching of ribs on the venter and the whorl section) to some *Prodichotomites* species is a matter of convergent evolution (i.e. homoeomorphy). *Prodichotomites* lacks a funnel-like umbilicus and the above described habit of rib bundling.

A. aff. *sverdrupi* exhibits also some convergent similarities with the early whorls of *P. canadensis* (Pl. 31, fig. 1A, 1B). In this case the differences consist in its funnel-like, more narrow umbilicus, in much more numerous bullae, and a different rib bundling habit.

Stratigraphic relationships and age. No information is available about the exact geographic location and stratigraphic position of *A*. aff. *sverdrupi*, which was found by the Mobil Oil Co. of Canada Ltd. on the northern part of Amund Ringnes Island (GSC loc. 85059). However, because of the association with paratype of *A. sverdrupi* (GSC Cat. 77122), this specimen is believed to be derived from the equivalents of the beds 8-9 of Kemper (1977, Fig. 3) and to be of latest early Valanginian age (Figure 62).

Amundiptychites thorsteinssoni n. sp.

Pl. 56, figs. 1A-1D; Pl. 61, figs. 2A-2C; Pl. 62, fig. 3;
Pl. 63, figs. 1A-1C; Pl. 64, figs. 1A, 1B;
Figures 59b, 59c).

1977 *Virgatoptychites*? *thorsteinssoni* n. sp. Kemper, p. 5 (nomen nudum).

1979 *Amundiptychites thorsteinssoni* n. sp. Kemper and Jeletzky,p. 4 (nomen nudum).

Origin of name. For Dr. R. Thorsteinsson from ISPG, Geological Survey of Canada, Calgary in recognition of his outstanding contributions to the geological exploration of the Sverdrup Basin.

Holotype. Original of Pl. 61, figs. 2A-2C, etc; GSC Cat. 77135; GSC loc. 93753(3) (= Ke 76/11/7-9).

Material. Two specimens from the GSC loc. 93753 (= Ke 76/11/7-9), Amund Ringnes Island (North).

Locus typicus. Amund Ringnes Island, NW-part, Lat. 78°38’20’’N, Long. 97°56’W.

Stratum typicum. Upper Deer Bay Formation. Fossiliferous beds 7-9 of Kemper (1977, Fig. 3). Most likely derived from Beds 8-9 but could also be from Bed 7. Uppermost lower and, possibly, lowermost upper Valanginian.

Diagnosis. An *Amundiptychites* species combining large size with slender and narrowly ventered whorls which retain this habit throughout the ontogeny (perhaps with the exception of the still unknown innermost whorls). Sculpture becomes weakened on the flanks in the intermediate (beginning with shell diameters between 40 and 60 mm) and adult growth stages. This results in a *Neocraspedites*-like appearance of these stages, except for the strongly elevated and widely spaced bullae.

Measurements in mm.

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
GSC Cat. 77135*	135	32(24)	44(33)	59(44)	40	51

* All measurements are approximate only because the shell is appreciably deformed.

Description. The holotype is septate to the end and fragments of another septate whorl are attached to one flank, so that the terminal diameter of the phragmocone must have reached about 200 mm and that of the complete shell at least 300 mm.

The most characteristic feature of the species is the slender, discoidal shape of all its observable whorls, which are always considerably higher than wide. In the holotype, this is true of all five observable whorls, including the smallest, about 20 mm high whorl exposed in the umbilicus (Pl. 61, figs. 2A, 2B; Pl. 63, fig. 1C). The width/height ratio of about 137 per cent measured in its third before last whorl (Pl. 63, fig. 1B) is representative. The approximately equivalent, fairly strongly deformed last whorl of the paratype (Pl. 56, figs. 1A-1D) is appreciably thicker but also higher than wide. Otherwise this whorl agrees with the equivalent whorl of the holotype in every detail of its shape and proportions.

The venter forms a narrow arch and the flanks are very feebly convex in all studied growth stages (the lower flank of the earliest exposed whorl of the holotype is not visible; Pl. 63, fig. 1C). Therefore, they converge almost evenly all the way adventrally from their maximum width at the umbilical shoulder with the slightly convex, gently inclined (at about 60 degrees to the plane of symmetry) umbilical wall. The narrow umbilicus is shallow but funnel-like (as is typical of the genus) because of the strong involution of the shell, the whorls of which cover the preceding whorls to the umbilical shoudler.

In the holotype the bullae are low and ill-delimited to the shell diameter of about 140 mm. Then they rapidly become better defined, more elevated and more nearly rounded (Pl. 63, figs. 1A-1C). Their extensions on the umbilical wall are indistinct. However, a forward inclination is perceptible on the last preserved whorl (Pl. 61, fig. 2A, 2B; Pl. 62, fig. 3) which bears 12 strongly elevated, conical bullae. In the paratype (Pl. 56, fig. 1A) the bullae are delicate but elevated and distinctly sharp-topped on the oral half of the last whorl (at the shell diameter of about 90 mm).

In the earliest preserved growth stage (shell diameter about 35-40 mm; Pl. 61, fig. 2A, 2B; Pl. 63, fig. 1C) the supplementary ribs are fine and closely spaced. They do not appear to be fasciculate, though the junction points of secondary ribs and bullae are all concealed. Instead, they appear to form groups consisting of two secondaries, which bifurcate at about the same level (i.e. bidichotomous habit). Single intercalated ribs either precede such bundles or occur between their bifurcating elements. The next older sculptural stage is visible in the last whorl of the paratype (Pl. 56, figs. 1A-1D) estimated to represent the shell diameter of 50 to 60 mm; its bundling habit is distinctly fasciculate at the whorl's beginning with the average of 5 supplementary ribs per bundle. These ribs are just as fine and closely spaced as those of the preceding sculptural stage (Pl. 63, fig. 1C). Farther adorally, one side of the last halfwhorl bears a similar fasciculate ornament (Pl. 56, fig. 1B). However, its other side (Pl. 56, fig. 1A) has 2 to 3 secondaries per bulla, which mostly bifurcate on the adventral half of the flank but can also split into 3 tertiary ribs. Solitary bifurcating ribs are intercalated between the bundles. The supplementary ribs are feebly arched forward on the venter which they cross without weakening. These supplementaries are distinctly coarser and more widely spaced than those of the early part of the whorl. The early weakening of the sculpture between the bullae and the flank's middle, which is particularly characteristic of the species, is already apparent on the oral part of this whorl. In the holotype, the comparably fine and dense supplementary ribs are so strongly weakened on the flank by an about 60-70 mm shell diameter (Pl. 63, figs. 1B, 1C) that their mode of bundling is no longer clearly discernible, though it appears to be fasciculate. This ornament appears to be even more strongly weakened by the shell diameter of about 100 mm and is all but absent on the last preserved whorl (Pl. 61, fig. 1A; Pl. 62, fig. 3). The mostly strengthened bullae of this advanced growth stage are opposed by a "crown" of relatively coarsened and sparsened supplementary ribs restricted to the ventral region. These supplementaries are distinctly forward bent on this and the earlier whorls of the holotype (Pl. 63, fig. 1A, 1B; Pl. 64, fig. 1A, 1B); they are nowhere weakened on the venter.

The presumably advanced adult external suture line visible on the last two whorls of the holotype (Pl. 61, fig. 2C; Figure 59b) consists of a ventral, two lateral, and five auxiliary lobes. The second auxiliary lies directly beneath the outer part of the bulla while the third to fifth auxiliaries are crowded on the umbilical wall. The lobes decrease gradually in size towards the umbilical seam; all are long, relatively narrow, approximately parallel-sided, and moderately deeply denticulate. The degree and depth of the denticulation decreases gradually adumbilically but even the fifth auxiliary is denticulated rather than simply notched (Pl. 61; fig. 2C; Figure 59b). All lateral saddles are noticeably to considerably more narrow than the preceding lobes, except for the fifth which is exceptionally wide and occupies all of the rounded umbilical shoulder (Pl. 61, figs. 2A, 2C; Figure 59b). The imaginary line joining the tops of saddles is forward arched; it ascends at 10 to 15 degrees over the first two saddles and the second lateral lobe, then turns around rapidly over the third and fourth lateral saddles until it becomes subradially oriented over the second auxiliary lobe; this course is then maintained to the umbilical seam.

The well and completely preserved external suture line of the paratype (Figure 59c) differs from that of the holotype in a considerably lesser degree of denticulation of all its elements, a relatively shorter and sturdier proportions of all lobes, a relatively considerably greater width of all lateral saddles, and the presence of only four auxiliary lobes. The reduced number of auxiliary lobes indicates the late juvenile character of this suture line. The imaginary line joining the tops of the first and second lateral saddles is approximately straight and ascendant at 10 to 15 degrees in relation to the corresponding radius; then it turns around over the third lateral saddle, becomes only slightly ascendant (less than 5 degrees) and maintains this course to the umbilical seam remaining approximately straight.

Affinities and differences. A. thorsteinssoni is a discoidal species which differs from *A. sverdrupi* in its considerably more slender whorls and a, presumably, much shorter duration of the tubular-shaped, evolute juvenile growth stage. The latter could only be present in the still unstudied early juvenile whorls with the shell diameter less than 35 mm. It is very distinct from the thick-whorled *A. fasciatus* and these two morphological extremes differ also in the number of auxiliary lobes.

The recently described Spitsbergen ammonite "*Neocraspedites*" *gratissimus* Yershova (1980, p. 74-75, Pl. IV, fig. 1; Pl. V, figs. 1a-1b) resembles very closely *A. thorsteinssoni* in the general shape and proportions of its shell and its sculpture. This ammonite is definitely not a *Neocraspedites* because of the presence of constrictions (Yershova, 1980, p. 74, Pl. V, fig. 2b). It appears to be, instead, an early and aberrant representative of *Amundiptychites* connecting it with the ancestral *Astieriptychites* (see p. 191 for further details). Yershova's (l. cit.) poor figures and brief description do not permit a comprehensive comparison of *A. thorsteinssoni* with *A. gratissimus*. However, the two are definitely not conspecific. The flanks of *A. gratissimus* become smooth at a considerably smaller shell diameter than those of the Canadian form. Furthermore, the division points of its primaries are situated considerably higher on the flank than those of the equivalent growth stages of *A. thorsteinssoni* (compare Pl. 56, figs. 1A, 1B; Pl. 61, figs. 2A, 2B with Yershova's, 1980, Pl. IV, fig. 1; Pl. V, figs. 1a, 2a). Finally, and most significantly, *A. gratissimus* has constrictions that are not known to occur either in *A. thorsteinssoni* or in any other Canadian *Amundiptychites* forms. Because of the appreciably older, late early Valanginian age of *A. gratissimus*, this presence of *Astieriptychites*-like constrictions suggests its being a transitional form connecting the essentially early Valanginian *Astieriptychites* with the early late Valanginian *Amundiptychites*. It could be a direct ancestor of *A. thorsteinssoni*.

Superficial similarity of *A. thorsteinssoni* to *Prodichotomites glaber* n. sp. is a matter of convergence only. *P. glaber* has a step-like umbilicus, a steeper umbilical wall and an entirely different, typically *Prodichotomites*-like sculpture. This is characterized by a larger number of bullae which does not change much in the course of the ontogeny. Furthermore, *P. glaber* has only three auxiliary lobes.

Amundiptychites fasciatus, n. sp.

Pl. 55, fig. 2A-2D; Pl. 56, fig. 2A-2C; Figures 60a, 60b.

Origin of name. After the *Olcostephanus*-like bundled, fasciculate (from lat. =*fasciatus*) secondary ribs.

Holotype. The original of Pl. 55, figs. 2A-2D; Figure 60a. GSC Cat. 77124.

Material. Two specimens from Amund Ringnes Island: 1. GSC loc. 93867 (Ke 76/11/7); and 2. GSC loc. 93753(6) (Ke 76/11/7-9)

Locus typicus. Amund Ringnes Island, NW part of the island, Lat. 78°38'20"N; Long. 97°56'W.

Stratum typicum. Upper Deer Bay Formation, fossiliferous beds 7-9 of Kemper (1977, Fig. 3). Uppermost Lower Valanginian (i.e. *Polyptychites tschekanovskii* Beds of Kemper and Jeletzky, 1979, p. 13, Figures 1, 9) but ranges higher up into the basal Upper Valanginian bed 7 (i.e. *Ringnesiceras* (*Ringnesiceras*) *pseudopolyptychum* Beds of Kemper and Jeletzky, 1979, p. 13, Figures 1, 9).

Diagnosis. A species of *Amundiptychites* characterized by broad (wider than high) but relatively narrow-ventered (narrowly arched) early and intermediate whorls. The relatively fine sculpture consists mostly of quasi-fasciculate rib bundles. The external suture line has three to four auxiliary lobes.

Measurements in mm.

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
GSC 77124 (Holotype)	93	26(28)	31(33)	37(40)	37	47
GSC 77126	82	21(26)	24(29)	36(44)	33	41

Description. The holotype and the paratype are septate to the end at their respective terminal diameters of 80 and 100 mm, so that it is impossible to say anything about the size of the adult shell. The whorls are always wider than high with the width/height ratio varying approximately from 81 to 73 per cent. However, they have a venter which is rather narrowly rounded for the Polyptychitinae. The venter of the paratype (Pl. 56, fig. 2C) is appreciably wider than that of the holotype (Pl. 55, fig. 2D). The increase of the width and the height of the whorls is relatively small; it is greater in the paratype than in the holotype. The umbilical shoulder is rounded and merges into a convex and at first only moderately steeply oriented umbilical wall. This wall becomes distinctly steeper in the last preserved whorl. The very involute character of the whorls (the last preserved whorl covers 85 per cent of the preceding whorl) and their extension to the rounded umbilical shoulder, result in an extremely funnel-like umbilicus, such as is present in all species of *Amundiptychites*.

The last preserved whorl of the holotype (Pl. 55, fig. 2A) carries 18 bullae while the preceding one carries 19 or 20. The last whorl of the paratype (Pl. 56, fig. 2B) carries about 16 bullae. The bullae are delicate. The bullae of the earlier whorls extend radially onto the gently inclined umbilical wall. However, on the first before last whorl, their extensions are not oriented radially any more but are slightly comma-like in the holotype and pronouncedly comma-like in the paratype in which they are also relatively higher and more acute. On the last preserved whorl the extensions of the bullae on the umbilical wall disappear in both specimens as the bullae themselves become more elevated.

Only the ribbing of the last preserved whorl is known. The initially polyptychitid ribbing is relatively finer in the holotype (Pl. 55, figs. 2A-2D) than in the paratype (Pl. 56, figs. 2A-2C). In both specimens the bundles of polyptychous type with 5 supplementary ribs alternate with other bundles which consist of two bifurcating secondaries with the addition of one intercalated single rib in front of the bundle. On the last halfwhorl the sculpture is approximately fasciculate at first. Then begins a distinct weakening of the ribbing between the bullae and the middle of the flank resulting in the opposition of the bullae to the "crown" of relatively refined supplementary ribs occupying the upper flank and the venter. The supplementary ribs are slightly arched on the venter.

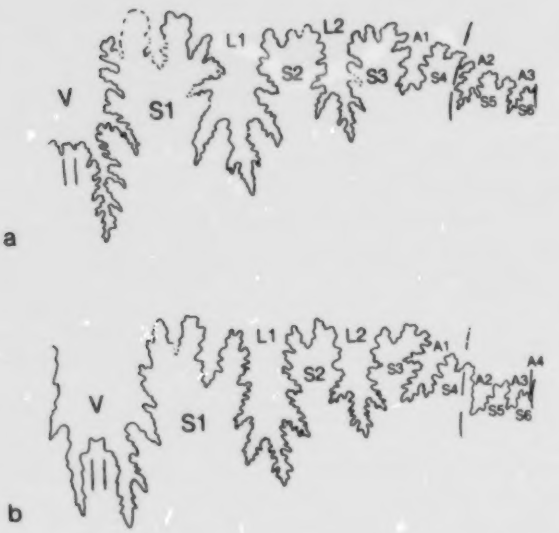


Figure 60. The presumably early adult external suture lines of *Amundiptychites fasciatus* n.sp. **a**. Holotype, GSC Cat. 77124 (Pl. 55, fig. 2) at an approximate whorl diameter of 44 mm (at the oral end of the whorl); **b**. Paratype, GSC Cat. 77126 (Pl. 56, fig. 2). At the approximate whorl diameter of 40 mm. Both figures x 1 (approximately).

The external suture line of the holotype (Figure 60a) is well preserved only at its oral end, all earlier sutures being deeply weathered (Pl. 55, figs. 2A, 2D). This presumably early adult suture resembles closely the late juvenile suture of *A. thorsteinssoni* exposed on the comparably large, last preserved whorl of its paratype (Figure 59c) in its similarly simple denticulation, similarly wide saddles, and similar orientation. However, it has only three auxiliary lobes and all of its lobes are much more slender than their counterparts in *A. thorsteinssoni*'s suture. Furthermore, its second and third auxiliaries are relatively larger and considerably more deeply denticulated structures. Finally, the *A. fasciatus* suture has only two lateral lobes and the first auxiliary lobe on the flank with the umbilical shoulder transecting the adumbilical quarter of the fourth lateral saddle (Figure 60a).

The equally well preserved last suture of the paratype of *A. fasciatus* (Pl. 56, fig. 2A; Figure 60b) only differs from the approximately equivalent suture of the holotype in the presence of an only partly exposed fourth auxiliary lobe at the umbilical seam. This smail and simple, roundtipped structure is similar to the fourth auxiliary lobe of the late juvenile suture of the paratype of *A. thorsteinssoni* (Figure 59c) in every respect.

These two presumably early adult sutures of *A. fasciatus* are similar to the adult and earlier external sutures of *Astieriptychites* (compare Figures 58b, 58c) in all of their taxonomically significant features.

Affinities and differences. A. fasciatus comprises the broader forms of the genus, though the species is incompletely known because no adult growth stages have been found. In spite of the great width of the whorl, there is a tendency to develop a relatively narrowly arched venter. Furthermore, the species is distinguished by an approximately fasciculate mode of bundling in the intermediate growth stages and a tendency to weakening of the sculpture in combination with an apparently lesser number of auxiliaries in the external suture line.

The differences from *A. sverdrupi* consist particularly in the inferred shorter duration of the tubular-shaped juvenile growth stage, broader whorls in the equivalent growth stages, a more narrowly arched venter and a relatively deeper, still more pronouncedly funnel-like umbilicus. Furthermore the presumably early adult external suture line of *A. fasciatus* has only 3 to 4 auxiliary lobes as compared with 4 to 5 in the equivalent and advanced adult suture lines (Figures 58d, 59a) of *A. sverdrupi*.

A. fasciatus has much broader whorls than the narrow-whorled extreme form of the genus — *A. thorsteinssoni*. The distinctions from *Amundiptychites* aff. *A. sverdrupi* are discussed in its description. The differences from the early whorls of *Polyptychites canadensis* species group consist in the funnel-like venter, much more numerous bullae and the quasi-fasciculate bundling rib style.

The variability of the above described external suture lines of *A. fasciatus* and the lack of data about the character of its more advanced whorls and sutures makes it uncertain whether the lesser number of auxiliaries (three to four) is a specifically diagnostic feature. It is also impossible to demonstrate that the sutures studied are early adult rather than late juvenile sutures. However, these conclusions are tentatively considered to be valid because of the generally conservative, rather *Astieriptychites*-like morphology of *Amundiptychites fasciatus* (e.g. its broader whorl section, prevalence of fasciculate bundling habit, etc.). This species appears to be the most primitive representative of *Amundiptychites* and connects this genus with the more slender representatives of the ancestral *Astieriptychites* (e.g. *A. mirus* Yershova 1980).

Subfamily SIMBIRSKITINAE Spath 1924
Ringnesiceras Kemper and Jeletzky 1979

Type species. Ringnesiceras amundense Kemper and Jeletzky 1979.

Derivation of name. From the discovery of the original material of the genus on Ellef and Amund Ringnes Islands of the Sverdrup Archipelago, N.W.T. (Kemper and Jeletzky, 1979, p. 5).

Diagnosis. Ammonites in which *Simbirskites*-like primary ribs and tubercles are present in the intermediate growth stages only. Polyptychitinid bullae occur instead of these tuberculate primaries in the preceding juvenile and the succeeding advanced growth stages. The external suture line has three to four auxiliary lobes and is either subradially oriented or somewhat ascendant, except in the weakly descendant auxiliary part. Secondary ribs tend to form virgatoptychitid rather than polyptychitid or simbirskitid bundles; they are bent forward on the venter as in *Dichotomites* and *Prodichotomites*. The shape and proportions of the early whorls resemble those of coronate *Simbirskites* while the intermediate whorls gradually become more and more slender and *Prodichotomites*-like.

Remarks. The shape of the whorl and the ornamentation of the intermediate whorls of *Ringnesiceras* resemble those of the simbirskitinid genus *Pavlovites* described by Aristov (1967) and Ivanov and Aristov (1969) from the Yaroslavl Province in Central Russia. Like *Ringnesiceras*, this genus combines morphological features of *Polyptychites* and *Simbirskites*. However, *Ringnesiceras* differs sharply from *Pavlovites* and all other known simbirskitinid genera in the advanced polyptychitinid character of its external suture line which has three to four auxiliary lobes. The suture line of *Pavlovites*, *Gorodzovia*, *Subspeetoniceras* and *Simbirskites* sensu lato (i.e. of all its subgenera) has, in contrast, only two auxiliary lobes and is distinctly to markedly suspensive in the auxiliary part.

Another morphological distinction of *Ringnesiceras* is the non-simbirskitinid, predominantly virgatoptychous bundling habit of secondary ribs in the early and advanced growth stages which may also have a somewhat polyptychous arrangement (see descriptions of individual species for further details). Yet another distinctive morphological feature of *Ringnesiceras* is a relatively to very broad (almost euryptychitid in *R. amundense* (see Bogoslovsky, 1902, Pl. XIV, figs. 4a, 6b) and *R.* (*R.*) *tozeri* (see Kemper and Jeletzky, 1979, Pl. 2, fig. 3b, 4c and Jeletzky, 1973, Pl. 2, Fig. 1c)), almost semicircular cross-section of the early whorls. This feature is particularly important in ruling out a direct genetic connection of *Ringnesiceras* with the superficially similar *Prodichotomites* in which the early whorls have a characteristically slender cross-section. These two genera differ also in the sculpture as *Prodichotomites* does not develop simbirskitiform primary ribs in any growth stage.

Ringnesiceras occurs in considerably older beds than any other simbirskitinid genus known. It is associated with *Homolsomites* cf. and aff. *H. quatsinoensis* (Whiteaves), *Buchia* ex aff. *inflata-sublaevis* (including *B. bulloides* Lahusen and *B.* n. sp. aff. *inflata* Jeletzky) and locally with *B. crassicollis* (Keyserling) sensu stricto. This fauna is diagnostic of the lower upper Valanginian zone of *Buchia* ex gr. *inflata-sublaevis* throughout Arctic and Western North America (see Jeletzky, 1973, Fig. 3 and the stratigraphic section of this paper for further details). All other presently known simbirskitinid genera, in contrast, are restricted to the lower to upper Hauterivian rocks (i.e. Wright in Arkell et al., 1957, p. L350; Rawson, 1971, p. 69-80, Fig. 9; Bahr, 1964, p. 166, Appendix 6).

Aristov (1967) and Ivanov and Aristov (1969) attempted to interpret *Pavlovites* and other simbirskitinid genera from the Lower Cretaceous rocks of Yaroslavl (e.g. *Gorodzovia* and *Subspeetoniceras*) as early Hauterivian ancestors of *Simbirskites* sensu lato. However, their conclusions were subsequently queried following a detailed stratigraphic and palaeontological study of this erratic block by Gol'bert et al. (1977). These workers concluded that the unit containing *Pavlovites*, *Gorodzovia* and *Subspeetoniceras* is separated from the underlying allegedly lower Hauterivian (in the writers' opinion upper Valanginian) unit containing "*Homolsomites*" *ivanovi* Aristov (actually a *Neocraspedites*-like representative of *Prodichotomites*; see Aristov, 1974, p. 152, Pl. XIV, figs. 1-2, Pl. XV, figs. 1-3 and pages 112-117 of this paper) and *Buchia* ex gr. *crassicollis-sublaevis* by a regional hiatus. They have, furthermore, discovered that the Yaroslavl fauna of simbirskitinids described by Aristov (1967) and Ivanov and Aristov (1969) occurs about 8 m stratigraphically above the hiatus and that the basal bed of the unit containing it carries young shells of other simbirskitinids. These simbirskitinids were identified as *Speetoniceras* by Gol'bert et al. (1977, p. 80). These data indicate that the Yaroslavl fauna of simbirskitinids is of late rather than early Hauterivian age. There is accordingly no reason to interpret the early late Valanginian *Ringnesiceras* as an immediate ancestor of *Pavlovites*, especially as their external suture lines are quite dissimilar. *Pavlovites* is, therefore, more likely a shortlived, late evolutionary offshoot of the main simbirskitinid lineage which became superficially similar to the considerably earlier *Ringnesiceras*.

The *Ringnesiceras* species of Sverdrup Basin are characterized by a great number (± 23) of slender and sharp-topped primary ribs which have lost the bullate habitus of their polyptychitinid predecessors at least in their middle growth stages. This modification was effected by the stretching of these ribs in the adventral direction which was naturally accompanied by a displacement of the starting point of the bundle of secondary ribs toward the middle of the flank. These processes, furthermore, were accompanied by an elevation of the adventral parts of the primary ribs. The combination of these three processes produced simbirskitiform primary ribs of *Ringnesiceras*. The acute, truly tubercular shape of the above-mentioned adventral elevations, which is characteristic of the primary ribs of true *Simbirskites*, tends to be imperfectly developed in *Ringnesiceras* and to be present only in its advanced representatives. In combination with the older age of *Ringnesiceras*, this indicates that its primary ribs represent an initial stage of the development of the simbirskitiform primary ribs. This inferred early phase of the simbirskitinid phylogeny is also characterized by the replacement of simbirskitiform primaries by normally bullate primaries in the late growth stages of *Ringnesiceras*. This development is completely unknown in the *Simbirskites*. The early growth stages of *Ringnesiceras* also have regular polyptychitiform bullae instead of simbirskitiform primaries. The evolutionary development of the typical *Simbirskites*-like primaries out of the polyptychitiform bullae follows, therefore, a proterogenetic (or prophetic; Pavlow, 1901, p. 62-63) mode.

Polyptychites ex gr. *canadensis* was suggested to be the ancestral stock of *Ringnesiceras* by Kemper and Jeletzky (1979, p. 6, 8, Figure 8). However, the constant presence of low and broad *Euryptychites*-like early whorls in this genus (e.g. Pl. 59, fig. 1) appears to contradict this idea and to suggest its derivation from *Polyptychites* ex gr. *michalskii* instead. According to this interpretation, the oldest and most primitive representatives of *Ringnesiceras* (*Ringnesiceras*) — *R.* (*R.*) *pseudopolyptychum* and *R.* (*R.*) *amundense* — arose from *P.* ex gr. *michalskii* by the lengthening of primaries and their thickening at the branching points. Because of the endemic character of *Ringnesiceras* (see below), this process probably took place in the Sverdrup Basin. However, *P.* ex gr. *michalskii* was not yet found in the Sverdrup Basin.

The oldest known *Simbirskites* (*Milanowskia*) ex gr. *concinnus-staffi* Wedekind from the lower-upper Hauterivian boundary beds are the most likely descendants of advanced *Ringnesiceras*, such as *R. tozeri*. This is suggested by the similarity of the ribbing habit of juvenile whorls of *R. tozeri* (see Pl. 52, figs. 2, 3) to that of the similar-sized whorls of these *Simbirskites* (*Milanowskia*) forms (e.g. Rawson, 1971, Pl. 3, figs. 1a, 4). Furthermore, their distance in time favors this idea.

The marked distinctions of the external suture line of these *Simbirskites* (*Milanowskia*) from that of *Ringnesiceras* sensu stricto may be interpreted as a result of its gradual reduction in the course of evolution of the still unknown early Hauterivian representatives of Simbirskitinae.

The inferred *Ringnesiceras-Simbirskites* sensu stricto lineage appears to be an important stage of evolution of the Early Cretaceous Perisphinctacea which connects its subfamilies Polyptychitinae and Simbirskitinae. The existence of such connecting links between these two subfamilies in the Arctic region was already suggested by Pavlow (1902, p. 42; 1914, p. 68) who states in the latter paper (Jeletzky's translation from Russian): "It must be taken into the consideration that I have already made a suggestion about a possible association of the first *Simbirskites* with the representatives of genus *Polyptychites* in the Pechora Basin (Pavlow, 1902, p. 42). These beds may prove to be equivalents of the middle Neocomian of western Europe (Pavlow, 1902, p. 42)".

It appears logical to interpret the older, morphologically most primitive representatives of the genus (i.e. *R. pseudopolyptychum* and *R. amundense*) as direct ancestors of its younger, morphologically more advanced representatives (i.e. *R. tozeri* and the subgenus *Elleficeras*). These data indicate that *Ringnesiceras* is an endemic lineage which arose and evolved in the Sverdrup Basin throughout the early late Valanginian and part or ?all of the late late Valanginian (Kemper and Jeletzky, 1979, p. 6, Figure 8; this paper, Figure 11).

The early Hauterivian and ?latest Valanginian evolutionary history of *Ringnesiceras* and its inferred transmutation into coronate simbirskitinids must have taken place elsewhere in the Arctic following the apparently complete draining of the Sverdrup Basin and its transformation into a deltaic-alluvial lowland and a source area (i.e. in the marginal parts) in the latest Valanginian or ?earliest Hauterivian.

The Pechora Province ammonites described and figured by Bogoslovsky (1902, Pl. XIV, figs. 3-5) as *Olcostephanus neritzensis* could be connecting links between *Ringnesiceras* and *Simbirskites* sensu lato. Their stratigraphic position in the profile is, however, unknown which precludes any definitive decision concerning their phylogenetic position within this lineage.

In addition to its above-discussed principal lineage (e.g. *R. pseudopolyptychum* → *R. amundense* → *R. tozeri*), *Ringnesiceras* apparently developed some phylogenetic offshoots. The most important of these is *Elleficeras* Kemper and Jeletzky 1979 which is described below. This subgenus differs from the subgenus *Ringnesiceras* sensu stricto in a considerably more slender and higher proportions of the whorls at intermediate and advanced growth stages. The sturdy, subcircular whorl cross-section is restricted to the very early growth stages and the adult external suture line has no less than four auxiliary lobes. This subgenus *Elleficeras* appears to be derived from *R.* (*R.*) *pseudopolyptychum* which also is known to have four auxiliary lobes.

Although *Ringnesiceras* was apparently an endemic of the Sverdrup Basin, it does not seem to be restricted to it. As pointed out in the description of individual Canadian species of the subgenera *Ringnesiceras* sensu stricto and *Elleficeras*, *Ringnesiceras* (*Ringnesiceras*) *amundense* appears to be present in the Valanginian rocks of Pechora Province in the European part of the Soviet Union where it was identified as *Olcostephanus* (sensu lato) spp. by Bogoslovsky (1902). Furthermore, it is probable that *R.* (*R.*) *pseudopolyptychum* is represented by some specimens from the basal upper Valanginian of northern Soviet Union which were identified as *Polyptychites* cf. or aff. *P. polyptychus* by Soviet workers recently. Finally *R.* (*R.*) *tozeri* occurs in Northern Siberia where it was misinterpreted as *Homolsomites bojarkensis* by Shulgina (1965, Pl. IV, fig. 1). These data suggest that the Canadian *Ringnesiceras* species are widespread guide fossils of the late Valanginian in the Arctic regions of the Boreal Realm.

Subgenus *Ringnesiceras* (*Ringnesiceras*)
Kemper and Jeletzky 1979.

Type species. As for the genus *Ringnesiceras*.

Diagnosis. *Ringnesiceras* forms in which the juvenile growth stage characterized by sturdy and relatively to very broad, almost semicircular cross-section of the whorl is unusually prolonged (up to shell diameters of 50 mm or somewhat more). The advanced growth stages are characterized by whorl cross-sections which are either wider than high or not much higher than wide. These advanced cross-sections are always considerably sturdier and lower than the equivalent cross-sections of the subgenus *Elleficeras*.

Remarks. See in the descriptions of the genus *Ringnesiceras* and subgenus *Elleficeras*.

Ringnesiceras (*Ringnesiceras*) *amundense*
Kemper and Jeletzky 1979

Pl. 57, fig. 3; Pl. 58, figs. 2A-2C; Pl. 58, figs. 3A-3B;
Figure 61a.

1902 *Olcostephanus* cf. *polyptychus* Bogoslovsky, p. 45, 46, 132, 133; Pl. 13, figures 2a-2c, 5a-5b, 6a-6b.

1902 *Olcostephanus* cf. *keyserlingi* Bogoslovsky, p. 46, 47, 133; Plate 13, figures 4a, 4b.

*1979 *Ringnesiceras* (*Ringnesiceras*) *amundense* Kemper and Jeletzky, p. 7, 8; Plate 1, figure 2a, 2b; Figure 4.

Holotype. The specimen GSC Cat. 61756 originally figured by Kemper and Jeletzky (1979, Pl. 1, figure 2a, 2b, Figure 4) and reproduced herein Plate 58, figure 2A-2C; Figure 61a.

Origin of name. From the occurrence of the type specimen on Amund Ringnes Island, N.W.T.

Material. Two well preserved specimens GSC 61756 and 77128 from GSC loc. 93755 (Ke 76/11/5) on Amund Ringnes Island. Four specimens from Pechora Basin, European part of USSR (see in the synonymy).

Locus typicus. Amund Ringnes Island, northwestern part; Lat. 78°38'20"N; Long. 97°56'W.

Stratum typicum. GSC loc. 93755. Upper Deer Bay Formation, fossiliferous layer 5 of Kemper (1977, Figure 3). Lower, but not the basal upper Valanginian.

Diagnosis. A small *Ringnesiceras* (*Ringnesiceras*) species, the shells of which are characterized by the sturdiest and widest whorl cross-section known in the subgenus *Ringnesiceras*. This cross-section does not become discoidal in the adult growth stage. The umbilicus is wider than that of the corresponding growth stages of any other species known. The uniquely simple and stubby-lobed adult external suture line has two to three auxiliary lobes.

Measurements in mm.

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
GSC Cat. 61756 (Holotype)	52	18(35)	17(33)	19(37)	23	28(?)
GSC Cat. 77128	49	15(31)	15(31)	19(39)	(18?)	21(?)

Description. The holotype is small with a maximum shell diameter of 58 mm. Further preparation of this specimen since the species was first described has revealed that its two oralmost sutures are considerably more crowded than the earlier ones. The last quarter whorl is devoid of suture lines and represents the beginning of the living chamber. The holotype is, therefore, an incompletely preserved adult, contrary to the conclusions of Kemper and Jeletzky (1979, p. 7, Fig. 4). The whorls are broad and low with the width considerably exceeding the height (see table of measurements). The exact shape of the roughly Roman arch-like cross-section is difficult to deduce as the last whorl is somewhat deformed. However, the distinctly convex flanks appear to converge increasingly adventrally from the level of the maximum width situated at the umbilical shoulder. This results in the venter being relatively somewhat more narrow than the regular Roman arch (Pl. 58, fig. 2C). The low, feebly convex, and relatively steeply oriented umbilical wall merges imperceptibly into the flank across a broadly rounded umbilical shoulder. The umbilicus is shallow and relatively wide (33 per cent). Because of a relatively low degree of involution, which comprises 60 per cent, and despite the pronouncedly rounded appearance of the umilical shoulder, the umbilicus is step-like and not funnel-like (Pl. 58, figs. 2B, 2C).

The adult external suture (Figure 61a) is rather simple with exceptionally short and stubby lobes the length of which only slightly (1½ times or less) exceeds their width. In addition to 2 lateral lobes it has two to three auxiliary lobes. The suture line is oriented slightly ascendant, except for the auxiliary part which is slightly descendant. The lateral and auxiliary lobes are symmetrically to slightly asymmetrically trifid, except for the only occasionally exposed third auxiliary lobe, which is a simple, stubby and rounded structure. The first lateral lobe is considerably shorter than the ventral lobe and the size of other lobes decreases more or less regularly all the way to the umbilical seam. The saddles are appreciably to considerably (up to two times) wider than the preceding lobes, except for the second lateral saddle which is only half as wide as the first lateral lobe.

The principal and secondary ribs are clearly differentiated. Whenever the shell is preserved, the principal ribs are slender and sharptopped partitions. There are 26 of them on the penultimate whorl and 23 on the last whorl. On the inner whorls they are radially oriented rather than comma-like. Then they become somewhat comma-like on the last whorl. However, even on the inner whorls they have feeble, slightly comma-like extensions which extend to the middle of the umbilical wall before petering out.

The primary ribs of *R*. (*R*.) *amundense* are distinctly elevated in the proximity of their point of subdivision into secondary ribs, in a *Simbirskites*-like fashion (Pl. 58, fig. 2A, 2B). However, these elevations still lack the acutely pointed shape characteristic of that genus. Furthermore, as happens in other *Ringnesiceras* species, these elevations disappear again in the advanced to adult growth stages. In these stages, if the observed trend is not misleading, the bullate adumbilical elevations may reappear again.

The style of bundling of secondary ribs is only observable on the last preserved whorl (Pl. 58, figs. 2A, 2B). Here is has a fundamentally virgatoptychous rather than polyptychous appearance. The bundles of the early half of this whorl consist of only three supplementaries, a simple anterior rib and a posterior rib which splits into two branches (a trivirgatitpartitous mode). On the last half of this whorl, an additional rib appears in some bundles, which either branches off the bulla in front of the bundle or is intercalated between the anterior and posterior ribs. This results in the appearance of quasivirgatoptychous rib bundles, which are especially common on the last quarter of that whorl. Generally speaking, the ribbing is fine and dense. On the ventral region the ribs are distinctly, even if not pronouncedly, arched forward (Pl. 58, fig. 2C).

The previously unfigured paratype GSC Cat. 77128 from GSC loc. 93755 (Ke 76/11/5) (Pl. 57, fig. 3; Pl. 58, figs. 3A, 3B) is small (maximum shell diameter 60 mm). The last segment of the last preserved whorl is definitely not septate and so represents the beginning of the presumably adult living chamber.

The last whorl of the paratype is somewhat deformed, so that it is not possible to obtain exact measurements of its width. However, the whorls are slender. The wh:wth ratio increases in the course of ontogeny (see table of measurements) but the width is still greater than the height at the end of the last whorl.

The venter is broadly rounded but not entirely semicircular at the beginning of the last whorl as its flanks are somewhat more strongly convergent adventrally. The cross section of the last half whorl is shaped like a half of an ellipse with a narrow arc. The largest diameter of this ellipse is situated at the level of the umbilical shoulder and its smaller arc forms the venter.

The umbilical shoulder is broadly rounded. The umbilical wall is very low, slightly convex and relatively steeply oriented. The moderately wide umbilicus has a shallow appearence.

The external suture line was not observed.

Primary ribs are slender, high and sharptopped. They are oriented radially. Addorsally these ribs peter out in the middle of the umbilical wall. Adventrally, they are damaged on the last preserved whorl. However, there is no doubt that they have a quasi-simbirskitiform habit there. However, spine-like elevations, such as are shown in the drawings of Bogoslovsky (1902) and can be designated as truly simbirskitiform structures, are absent in this paratype. The specimen has 12 primary ribs on the last half whorl and there are 22 such ribs on its penultimate whorl.

The sculpture is exceptionally regular: the posterior secondary rib bifurcates adventrally of the middle of the whorl while the anterior secondary rib remains simple and undivided. A simple intercalated secondary situated in front of the bundle was only observed once. The secondary and tertiary ribs are strongly arched forward on the ventral region (Pl. 58, fig. 3B).

The more slender of the specimens figured by Bogoslovsky (1902, p. 45, 46, 132, 133; Pl. 13, figs. 5, 6 non fig. 2) and included in the synonymy of *R.* (*R.*) *amundense* agree well with the Canadian paratype, except that their morphology is still more pronouncedly simbirskitiform. Bogoslovsky's (l. cit.) Figure 5a exhibits all signs of the adult growth stage. This specimen shows clearly that the simbirskitiform primary ribs of the early and intermediate growth stages are replaced by the polyptychitiform umbilical bullae in the adult. The specimen reproduced in Bogoslovsky's (l. cit.) Pl. 13, fig. 2 is a more slender and less densely ribbed variant.

Affinities and differences. The closely similar but considerably more slender-whorled ?*Ringnesiceras* (*Ringnesiceras*) aff. *amundense* (Pl. 59, figs. 1A, 1B) is a possible ancestor of *R.* (*R.*) *amundense*. Because of its broad whorls, wide umbilicus, and simple, stubbylobed adult external suture with only two to three auxiliary lobes *R.* (*R.*) *amundense* cannot be confused with any other *Ringnesiceras* species. Neither can it be confused with any *Polyptychites* species because of the quasisimbirskitiform appearance of its primary ribs.

The true Hauterivian *Simbirskites* have more coarse primary and supplementary ribs and, therefore, a lesser number of ribs per whorl. Their supplementary ribs form approximately fasciculate bundles, which consist of 2 to 3 secondaries in the intermediate and adult growth stages. There are no indications whatsoever of virgatoptychous or polyptychous bundling habit in *Simbirskites*. Finally, their suture has only two auxiliary lobes and is markedly suspensive.

Among the representatives of *Simbirskites*, only the coronate species, such as *S.* (*S.*) *decheni* (Roemer), are superficially similar to *R.* (*R.*) *amundense* as the bulk of *Simbirskites* forms have slender and discoidal shells but even the coronate *Simbirskites* are mostly more slender than *R.* (*R.*) *amundense*. However, *S.* (*S.*) *picteti* (Weerth) (compare Rawson, 1971, Pl. 1) is just as inflated as *R.* (*R.*) *amundense*.

The trivirgatitpartitous bundles and the distinct forward arching of the ribs on the venter of *R.* (*R.*) *amundense* remind one of the ribbing habit of *Dichotomites* s.str. However, these similarities are obviously of a homoeomorphic character only because of the simbirskitiform primary ribs and broader juvenile whorls of *Ringnesiceras* and a greater number of auxiliary lobes in *Dichotomites*.

Stratigraphic relationships and age. The two Canadian representatives of *R.* (*R.*) *amundense* were found in the bed 5 of the upper Deer Bay Formation (Kemper, 1977, fig. 3; Kemper and Jeletzky, 1979, p. 7, Fig. 1) and appear to be restricted to it. The fauna of that bed constitutes the *Ringnesiceras* (*Ringnesiceras*) *amundense* fauna of Kemper and Jeletzky (1979, p. 14, 15, Figs. 1, 9) that is of an early, but not earliest, late Valanginian age (Figure 62). The exact age of the Pechoran representatives of *R.* (R.) *amundense* is not known but presumed to be approximately the same as that of its Canadian representatives.

Ringnesiceras (*Ringnesiceras*) *pseudopolyptychum* Kemper and Jeletzky 1979

Pl. 57, figs. 1, 2; Pl. 58, fig. 1, figs. 4A, 4B; Pl. 59,
figs. 2A, 2B, 3A-3C; Pl. 60,
fig. 4; Figures 61b, 61c.

Synonymy

1977	*Dichotomites* (?*Prodichotomites*) *tozeri* (pars) Kemper, p. 5.
*1979	*Ringnesiceras* (*Ringnesiceras*) *pseudopolyptychum* Kemper and Jeletzky, p. 8, Pl. 2, figs. 2a-2c; Figures 5, 5a.

Origin of name. The specific name *pseudopolyptychum* was introduced to point out the superficial similarity, as opposed to true specific identify, of our form with *Polyptychites polyptychus* (Keyserling).

Holotype. Specimen GSC Cat. 61758 from GSC loc. 93871 originally figured by Kemper and Jeletzky (1979, Pl. 2, figs. 2a-2c; Figures 5, 5a) and reproduced herein in Pl. 57, fig. 1; Pl. 58, figs. 4A, 4B; Figures 61b, 61c.

Material. Four specimens from Ellef Ringnes Island, including two from GSC loc. 93870 and two from GSC loc. 93871. Furthermore, one specimen from GSC loc. 93755 and one from GSC loc. 93753 on Amund Ringnes Island.

Locus typicus. Ellef Ringnes Island, Sverdrup Archipelago, N.W.T., GSC loc. 93871.

Stratum typicum. GSC loc. 93755. Upper Deer Bay Formation. Fossiliferous bed 7 (Ke 76/3/-4) of Kemper (1977, Figure 3). Lowermost upper Valanginian (see Figure 62).

Diagnosis. Medium-sized species of *Ringnesiceras* (*Ringnesiceras*) combining a moderately narrow umbilicus (about 27 per cent of the shell diameter) with a feeble development or bare suggestion of tubercles on the simbirskitiform primary ribs of the intermediate growth stages. The secondary ribs of intermediate whorls are arranged in polyptychous bundles which arise either out of numerous, fine and high umbilical bullae or out of the simbirskitiform primary ribs. Cross-sections of juvenile whorls are broad and *Euryptychites*-like shaped while those of intermediate whorls are slender and higher than wide. The latter cross-sections have a flat-sided, discoidal shape. The early adult external suture line has four, somewhat underdeveloped auxiliary lobes.

Measurements in mm.

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
GSC Cat. 61758 (Holotype)	(84)	22(27)	(30)(36)	32(38)	(31)	37
GSC Cat. 77130	(119)	32(27)	(35)(29)	(51)(43)	(35)	(48)

Description. Though the preservation is good in some respects, it was not possible to obtain reliable measurements because of the deformation of most specimens. Except for the perhaps not quite adult holotype 61758 (Ke 76/3/-4), all specimens available are entirely septate. Therefore, it is not possible to obtain reliable data about the size of our species. Its adult shell diameter is believed to be in order of 150-200 mm.

Specimen GSC Cat. 77130 (Pl. 59, figs. 2A, 2B) is a fragment which provides an insight into the ontogenetic development of the species. The following height/width ratios have been measured on this specimen:

Shell diameter	wh 1	wh 2	wth 1	wth 2
30 mm	6	12	(11)	16
69 mm	24	—	26	—
last whorl:	—	48	—	41

The wh:wth ratio changes accordingly from 6:11 to 11:16 and 24:26 to 48:41. The whorls are accordingly twice as broad as they are high at first (until a shell diameter of about 20 mm). At a shell diameter of 70-80 mm they are as broad as they are high and soon thereafter higher than broad. This significant increase in the height of the whorls in the course of ontogeny results in a discoidal shape of adult shells (Pl. 57, fig. 1; Pl. 58, fig. 1). The whorl section changes accordingly. The at first *Euryptychites*-like and then broadly arched shape of the early whorls is replaced in the adult by a narrowly arched venter, which merges into the by now only slightly convex flanks.

The umbilical shoulder is moderately broadly rounded and merges gradually into a very low umbilical wall. This wall is relatively steep in the juvenile and intermediate growth stages but becomes more obliquely oriented in the adult. The umbilicus is moderately involute (27 per cent), shallow, and distinctly step-like (Pl. 57, fig. 2; Pl. 58, fig. 4A, 4B; Pl. 59, figs. 3A, 3B).

The external suture line of the holotype (Figure 61b) resembles closely that of *R.* (*R.*) *amundense*, except for being somewhat more strongly and deeply denticulated, and considerably more slender-lobed and for possessing four auxiliary lobes. However, the taxonomic reliability of this feature is somewhat uncertain. Judging by the rather scant material available, the adumbilicalmost part of the suture line, which includes the third and fourth axuiliaries, tends to be rather imperfectly differentiated and variably shaped. As indicated in Figures 61b, 61c, the third and fourth? auxiliary lobes are simple tack-like structures similar and subequal to the intervening lobule. Therefore, they can only be distinguished from the latter because of their position. An additional lobule may be present between the fourth auxiliary and the umbilical seam in those suture lines which are situated within the concave segments of the umbilical seam confined between the primary ribs of the preceding whorl (Figure 61c).

Like the whorl shape, the sculpture is subject to ontogenetic changes. The primaries are slender and high at first. They are, therefore, nothing more than stem-like primary ribs (Pl. 59, fig. 2A). They only become extended upward in the intermediate growth stages. They become still thicker on the penultimate and last whorls but remain relatively delicate for the genus. This slender expression of bullae is matched by their high number, which becomes reduced to 18-20 on the late intermediate to adult growth stages from 20-22 on the early intermediate growth stages. The orientation of primary ribs or bullae changes in the course of ontogeny. Generally, they are only slightly comma-like and peter out fast on the umbilical wall. However, a growth stage characterized by strong comma-like bends is intercalated at a shell diameter of approximately 50 mm (Pl. 59, figs. 3A, 3B). This stage, which was observed in all specimens studied, extends over one-quarter to one-half whorl. Therefore, it is undubitably a characteristic feature of the species. In these intermediate growth stages, the primary ribs may be distinctly elevated in the proximity of their point of subdivision, in a *Simbirskites* like fashion (e.g. Pl. 58, fig. 4A).

It was only possible to observe the ribbing from diameters of 50 to 60 mm upward. It is only known to be very fine at earlier growth stages. At diameters of 80 to 100 mm the ribbing habit is quasi-polyptychitid (Pl. 59, figs. 3A, 3B; Pl. 57, fig. 2; Pl. 58, figs. 4A, 4B). This means that the bundles average 5 supplementary ribs per bulla. However, bundles consisting of three supplementary ribs are intercalated between the former bundles. In the polyptychitid bundles two additional ribs split off in an oralward direction from the posterior rib while the anterior rib simply bifurcates. Rib bundles of this kind occur in the late preadult ontogeny of several *Polyptychites* species.

In *R.* (*R.*) *pseudopolyptychum* the above-mentioned sculpture is gradually replaced by an almost bi- to tridichotomous adult sculpture, as is clearly visible in Pl. 57, fig. 2. However, this sculpture is not strictly speaking bi- or tri-dichotomous as the branching points of the ribs are not situated at exactly the same level. The progressive differentiation of supplementary ribs into secondary and tertiary ribs is accompanied by the gradual elevation of the secondary ribs, which become relatively strengthened sculptural elements. The supplementary ribs are arched forward on the ventral region. This arching is more strongly developed in the juvenile growth stages.

Affinities and differences. The *Polyptychites*-like character of the sculpture of *R.* (*R.*) *pseudopolyptychum* combined with its being the oldest known representative of the genus and the subgenus suggest that it represents the

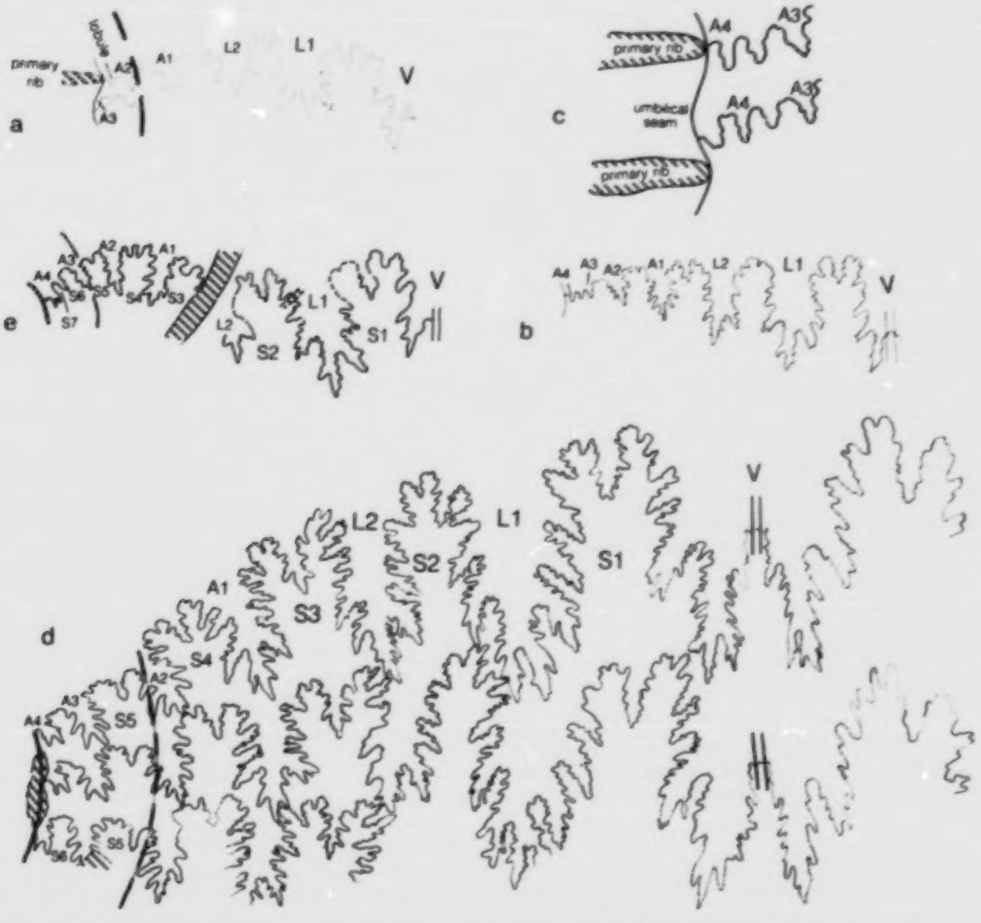


Figure 61. Adult external suture lines of *Ringnesiceras*. **a**. *R.* (*Ringnesiceras*) *amundense* Kemper and Jeletzky 1979. Holotype, GSC Cat. 61756 (Pl. 58, fig. 2), x 1. The suture observed at wh = 24 mm (appr.); **b**. *R.* (*Ringnesiceras*) *pseudopolyptychum* Kemper and Jeletzky 1979. Holotype, GSC Cat. 61758 (Pl. 57, fig. 1; Pl. 58, fig. 4). The probably early adult suture observed at wh = 17 mm (appr.), x 1; **c**. The same specimen as in b. Adumbilicalmost parts of adjacent, ?early adult sutures at wh = 13 mm (appr.), x 4 (approx.); **d**. *R.* (*Ringnesiceras*) *tozeri* Kemper and Jeletzky 1979. Holotype, GSC Cat. 33332 (Pl. 51, fig. 1). Advanced adult suture at wh = 80 mm (approx.), x 1; **e**. *R.* (*Elleficeras*) *ellefense* Kemper and Jeletzky 1979. Holotype, GSC Cat. 61757 (Pl. 60, fig. 3). Early adult suture observed at wh = 43 mm (approxim.), x 1.

rootform of *Ringnesiceras* morphologically and phylogenetically transitional from advanced representatives of *Polyptychites* sensu stricto (compare p. 199, 200).

Among the late early Valanginian *Polyptychites* forms of the Sverdrup Basin, *R.* (*R.*) *pseudopolyptychum* resembles most closely *P. tschekanovskii* described elsewhere in this paper. From this only homeomorph species *R.* (*R.*) *pseudopolyptychum* differs in the much more slender proportions of its shell and a greater number of auxiliary lobes.

R. (*R.*) *pseudopolyptychum* is but a homoeomorph of the sculpturally similar *Polyptychites polyptychus* (Keyserling) because of the presence of four auxiliary lobes instead of only two characteristic of the latter species (Pavlow, in Pavlow and Lamplugh, 1892, p. 477-78; Keyserling, 1846, p. 328; Pl. 22, fig. 9) and the presence of at least some simbirskitiform primary ribs with incipient to feeble tubercles in the intermediate growth stages. Furthermore, it differs from the true *Polyptychites polyptychus* in the gradual transformation of low and broad, semicircular-shaped early whorls into considerably higher than wide, flat-flanked and discus-shaped intermediate whorls. All above-mentioned distinctions are of generic rather than specific value, as pointed out earlier in the description of *Ringnesiceras*.

From other representatives of the subgenus *Ringnesiceras* sensu stricto *R.* (*R.*) *pseudopolyptychum* differs in:

1. Prevalence of polyptychitid bundling habit and comma-like polyptychitid bullae on the intermediate whorls combined with a relatively more limited and feeble development of simbirskitiform primary ribs and tubercles; and
2. Slender, considerably higher than wide and flat-flanked cross-section of intermediate and advanced whorls.

Stratigraphic relationships and age. As far as is known, *R.* (*R.*) *pseudopolyptychum* appears for the first time in bed 7 of Kemper's (1977, p. 5, Fig. 3) sections and is largely restricted to that bed, which overlies gradationally the uppermost lower Valanginian beds 8-9 containing the *Polyptychites tschekanovskii* fauna (Kemper and Jeletzky, 1979, p. 13, Figs. 1, 9). The ammonite fauna of bed 7 was, therefore, designated as the *Ringnesiceras* (*Ringnesiceras*) *pseudopolyptychum* fauna by Kemper and Jeletzky (1979, p. 13, 14, Figs. 1, 9). It must be noted, however, that *R.* (*R.*) *pseudopolyptychum* is not restricted to bed 7 but ascends locally into the next younger *Ringnesiceras* (*Ringnesiceras*) *amundense* Beds (Kemper and Jeletzky, 1979, p. 15, Figure 1).

Ringnesiceras (*Ringnesiceras*) *tozeri*
Kemper and Jeletzky 1979

Pl. 50, fig. 1; Pl. 51, figs. 1A-1D; Pl. 52, figs. 2A-2C, 3A-3C; Figure 61d.

Synonymy

1965	*Homolsomites bojarkensis* Shulgina, Pl. IV, fig. 1 (*non* Pl. I-III).
1973	*Polyptychites* (*Dichotomites*) aff. *bidichotomus* Jeletzky, p. 72, 73, Pl. 1, figs. 1a, 1b; Pl. 2, figs. 1a-1c; Pl. 3, fig. 1.
1975	*Dichotomites* (*Prodichotomites*) sp. Kemper, p. 248, 249.
1977	*Dichotomites* (*Prodichotomites*) *tozeri* Kemper, p. 5 (partim) (nomen nudum).
*1979	*Ringnesiceras* (*Ringnesiceras*) *tozeri* Kemper and Jeletzky, p. 9, 10, Pl. 2, figs. 3a, 3b, 4a-4c; Figure 6.

Origin of name. For E.T. Tozer of the ISPG, Geological Survey of Canada, Ottawa in recognition of his outstanding research of the Mesozoic geology and paleontology of Sverdrup Basin.

Holotype. The specimen GSC Cat. 33332 originally figured by Jeletzky (1973, Pl. 1, figs. 1a, 1b; Pl. 2, figs. 1a-1c; Pl. 3, fig. 1) and reproduced in this paper in Plate 50, fig. 1; Pl. 51, fig. 1A-1D; Figure 61d.

Material. One specimen from Ellef Ringnes Island (holotype). Two juvenile specimens from Amund Ringnes Island collected at GSC loc. 91297; Lat. 78°38'20"N; Long. 97°56'W. One specimen from the Khatanga Depression, northern Siberia (Shulgina, 1965, Pl. IV, fig. 1; this specimen only).

Locus typicus. Ellef Ringnes Island of the Sverdrup Archipelago, N.W.T. Exact locality unknown.

Stratum typicum. Upper Deer Bay Formation, beds situated ca. 60 m stratigraphically below the contact with the Isachsen Formation.

Diagnosis. A large-size (the largest phragmocone is estimated to have maximum shell diameter of at least 200 mm) *Ringnesiceras* sensu stricto species which differs from other representatives of the genus in more pronounced forward bends of secondary ribs in the venter of intermediate whorls. Furthermore, *R.* (*R.*) *tozeri* differs from the comparably large *R.* (*R.*) *pseudopolyptychum* in the appreciably more narrow and deeper umbilicus and a full development of four auxiliary lobes in the advanced external suture line. From the adult growth stages of *R.* (*R.*) *amundense*, *R.* (*R.*) *tozeri* differs in the much larger shell size, the presence of four auxiliary lobes, a more slender, adventrally narrowing cross-section, and an appreciably more narrowly rounded venter.

Measurements in mm.

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
GSC Cat. 61759 (1st paratype)	36	11(30)	11(30)	15(42)	13	15
GSC Cat. 61760 (2nd paratype)	33	9(27)	11(35)	14(47)	13	15

Description. The holotype consists of about one-quarter of the shell which permits a more or less limited insight into 4 preceding whorls. The specimen is septate throughout, which makes it impossible to make any firm conclusions about its adult shell diameter. However, this is estimated to reach at least 200 mm.

The whorl section changes strongly in the course of ontogeny (Pl. 50, fig. 1). The whorls are considerably wider than high until the shell diameter of 40 mm. It is impossible to obtain any measurements on the second before last and the earliest part of the penultimate preserved whorls but their cross-sections still remain wider than high. At the shell diameter of ca 110 mm occurs a gradual transition to whorls that are higher than wide. The wh 2:wth 2 ratio comprises here 51:47 mm. It is again impossible to make any measurements on the preserved fragment of the last whorl but its ratio wh:wth has a similar or a still greater value. The cross-section changes accordingly from an obtusely hoof-like to a discoidal one. It is at first (i.e. on the earliest preserved whorl; Pl. 50, fig. 1) broadly rounded and resembles that of adult *Polyptychites* ex gr. *hapkei-sphaeroidalis*. Later the ventral rounding becomes progressively more and more narrowly arched. The now less convex flanks become increasingly narrowly arched at the same time (Pl. 51, fig. 1C).

The flanks merge across a broadly rounded umbilical shoulder into a gently inclined umbilical wall which makes an approximately 60-70 degree angle with the plane of symmetry. Because of this gentle inclination of the umbilical wall and a very strong involution which amounts to about 80 percent of preceding whorls, the moderately narrow umbilicus is expressly funnel-like shaped.

The advanced adult external suture line of the last preserved whorl is considerably more strongly and deeply denticulated than the advanced and early adult suture lines of considerably to much smaller whorls of *R*. (*R*.) *amundense* and *R*. (*R*.) *pseudopolyptychum*. Furthermore, it is stronger retractive in its auxiliary part than are the other two suture lines. Finally, the adjacent external suture lines of *R*. (*R*.) *tozeri* are more closely spaced than those of the other two species and the lobes of succeeding lines mostly touch the saddles of the preceding lines (Figure 61d). Except for the advanced adult suture of *R*. (*R*.) *amundense* (Figure 61a), is not certain whether the above morphological distinctions are signficant at the species level or reflect age differences of the sutures concerned.

The external suture of *R*. (*R*.) *tozeri* has 4 fully developed auxiliary lobes in addition to the two lateral lobes. The umbilical seam cuts through the umbilical side of the fourth auxiliary (Figure 61d). The previously claimed presence of only three auxiliaries and the phylogenetic conclusions derived therefrom (Kemper and Jeletzky, 1979, p. 6, 10) are incorrect and must be abandoned.

As with the whorl shape and proportions, the sculpture exhibits pronounced changes in the course of the ontogeny of the holotype. Because of a damaged character of the umbilical zone of the third and second before last whorls only assumption can be made about their primary structures. Evidently they are not bullae but simbirskitiform primary ribs. On the penultimate and ultimate preserved whorls these ribs are transformed into low swellings of a bulla-like appearance. They are only feebly comma-like bent and peter out between the outer half and the outer third of the umbilical wall. These bullae cannot be reliably counted but their number appears to be more likely under than over 20 on each of the two last whorls.

The ribbing habit of the third and second before last whorls has, so far as it is recognizable, a basically trivirgatitpartitous character. The sculpture is weak and indistinctly developed on the two outer whorls where it is particularly weakened between the bullae and the middle of the flank. On the penultimate preserved whorl, this sculpture includes bidichotomous bundles, either with or without an additional intercalated secondary rib, in addition to the trivirgatitpartitous bundles (Pl. 51, fig. 1B). The weakening of the sculpture on the addorsal half of the flank of the last preserved whorl has progressed so far that it is no longer possible to make any reliable observations concerning its bundling habit (Pl. 51, fig. 1A). The supplementary ribs of that whorl are strongly arched forward on the uppermost flank and venter (Pl. 51, fig. 1B-1D).

The holotype exposes only parts of two intermediate, fully septate whorls. The previous intermediate and juvenile whorls are only observable in cross-section. The only exception is the earliest preserved whorl, of which only the impression of the venter is preserved (Pl. 50, fig. 1; Jeletzky, 1973, Pl. 2, fig. 1c). However, most of the juvenile growth stages concealed in the holotype are well exposed in two small specimens found on Amund Ringnes Island and figured herein (Pl. 52, figs. 2A-C, 3A-C). These specimens are assigned to *R*. (*R*.) *tozeri* as the shape and proportions of their cross-sections are closely similar to those of the corresponding whorls of the holotype. Furthermore, they were found at about the same level as the holotype. These two juvenile specimens exhibit only the beginning of the simbirskitinid sculptural growth stage near their oral end (Pl. 52, figs. 2A, 2B) where the simbirskitiform primaries and tubercles are either feebly developed or only suggested. The extent of this simbirskitinid growth stage and the morphology of its principal part remain unknown as neither the simbirskitiform primaries nor the simbirskitiform tubercles persist onto the innermost intermediate whorl fully exposed in the holotype (Jeletzky, 1973; Pl. 3, fig. 1; this paper, Pl. 51, fig. 1B). The first paratype (GSC Cat. No. 61759; Pl. 52, fig. 2A-2C) is the larger of these two small specimens. It is completely septate and well preserved. The width of the whorl is greater than its height at the beginning of the last preserved whorl. However, at the whorl's end it is already higher than wide (see Table of Measurements). Therefore, the transition to the slender whorls occurs considerably earlier in this paratype than it does in the holotype. The approximately half circular cross-section of the penultimate preserved whorl changes into a high-oval cross-section at the end of the last preserved whorl.

This specimen is interpreted as a slender variant of our species.

In accordance with the relatively lesser shell width of this paratype, its narrow umbilicus is shallower than that of the holotype. Furthermore, it is less funnel-like because of a lesser degree of involution (75 per cent). The broadly rounded umbilical shoulder grades imperceptibly in the low umbilical wall. Therefore, the umbilical shoulder and the gently inclined umbilical wall form an indivisible unit to the last whorl. On the last preserved whorl its more steeply oriented umbilical wall becomes a separate element. It is low and distinctly convex.

The primary elements of the sculpture are slender but high bullae to the beginning of the last half of the last whorl. On the second before last whorl they are directed backward on the umbilical wall. On the penultimate whorl they are approximately radially oriented and only peter out in the proximity of the seam. On the last preserved whorl they acquire comma-like bends. The comma-like extension of this growth stage is strongly inclined forward until it peters out approximately in the middle of the umbilical wall. The bullae of the first half of the last whorl are comma-like bent to the proximity of the branching points of secondary ribs and are distinctly elevated at this point.

The primary ribs extend in the ventral direction on the last half of the last preserved whorl. Therefore, they lose their bulla-like character there and become rather primary ribs. At that they begin to resemble the quasi-simbirskitiform primary ribs, which were already discussed in the description of *R.* (*R.*) *amundense*. It can be expected, that these simbirskitiform properties would be still better expressed on the not preserved, next outer growth stage of our specimen. The last preserved whorl carries 24 bullae or primary ribs whilst the penultimate whorl carries 21.

The ribbing habit is only visible on the last preserved whorl. It is fine and dense. On the apical half of this whorl it is trivirgatipartitous. On its oral part occur bundles with an additional rib in front. One of the bundles here consists of 2 bifurcating secondary ribs. The basic character of the rib bundling habit is rather virgatitpartitous than polyptychitid.

The second paratype (GSC Cat. 61760; Pl. 52, fig. 3A-3C) is so extraordinarily similar to the above described first paratype that it is unnecessary to describe it in any detail, except for mentioning its distinctly coarser and sparcer ribbing.

Affinities and differences. *R.* (*R.*) *tozeri* is the youngest known representative of *Ringnesiceras* and at the same time the youngest representative of the family Olcostephanidae known in the Valanginian rocks of the Sverdrup Basin. Neither of the other two *Ringnesiceras* sensu stricto species was found in the Tozeri Beds. The available material is scarce and fragmentary but its younger age and distinctive morphology leaves no doubt that *R.* (*R.*) *tozeri* is an independent species.

Morphological distinctions of *R.* (*R.*) *tozeri* from the other *Ringnesiceras* (*Ringnesiceras*) species have been discussed earlier.

The ammonite figured by Shulgina (1965, Plate IV, fig. 1) and misinterpreted as *Homolsomites bojarkensis* is a typical representative of *R.* (*R.*) *tozeri*. This is indicated by the well-developed umbilical bullae in combination with a narrow and deep but not involute umbilicus and the polyptychitinid external suture line. The last is similar to that of *R.* (*R.*) *tozeri* in the general appearance of lobes and saddles, distinctly suspensive character of the auxiliary part and presence of at least three auxiliary lobes. The biostratigraphic implications of this finding were discussed by Kemper and Jeletzky (1979, p. 16, Figure 9) and are summarized in the stratigraphic section.

Stratigraphic relationships and age. On Amund Ringnes Island *R.* (*R.*) *tozeri* has been found only in beds 2 and 4 of Kemper (1977, Fig. 3; this paper, Fig. 62). The holotype (from Ellef Ringnes Island) is derived from an approximately equivalent inverval, judging by its recorded stratigraphic position about 60 m below the contact with the Isachsen Formation. For further details see Figure 62.

?*Ringnesiceras* (*Ringnesiceras*) n. sp. aff. *amundense* Kemper and Jeletzky 1979,

Plate 59, fig. 1A, 1B.

Material. One well preserved specimen GSC Cat. 77129 from GSC loc. 93753 (= Ke 76/11/7-9).

Measurements in mm.

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
GSC Cat. 77129	54	18(33)	16(30)	22(41)	23	(28)

Description. The specimen has a maximum diameter of 63 mm. It is septate to the end, so its adult size is unknown. The beginning of the last preserved whorl is broadly arched and considerably wider than high (wh:wth = 16:23). However, this whorl rapidly becomes higher and narrower so that the ratio wh:wth becomes 22:28 already one-half whorl farther. The rounded umbilical shoulder grades into a strongly convex umbilical wall. The relatively wide umbilicus (33 per cent) is accordingly funnel-like.

The external suture line, that is generally speaking similar to that of *R.* (*R.*) *pseudopolyptychum*, has only 3 auxiliary lobes addorsally of two lateral lobes. This suggests its transitional character between the sutures of *R.* (*R.*) *amundense* and *R.* (*R.*) *pseudopolyptychum*.

The preserved whorls carry 22-23 slender and high bullae. So far as it is possible to see, these resemble somewhat the primary ribs of *Simbirskites* on the penultimate whorl (Pl. 59, fig. 1B). They become polyptychitinid-shaped, with the greatest height situated in the proximity of the umbilicus, only on the last preserved whorl. The bullae extend onto the umbilical wall where they disappear only on its inner third. These extensions are oriented distinctly radially and perpendicular to the direction of shell's growth.

The ribbing habit is predominantly polyptychous. As happens commonly in the genus *Polyptychites*, rib bundles with 5 supplementary ribs alternate with ones including 3 supplementary ribs. In the last bundles two supplementary, forwardly-directed ribs split off from the posterior rib. In the bundles including 5 supplementary ribs a bifurcating anterior element occurs in front of this trifurcate element.

The development of simbirskitiform primary ribs evidently proceeded in a proterogenetic fashion. This process was progressing farther in the considerably broader-whorled *R.* (*R.*) *amundense*.

As only a solitary, small representative of ?*Ringnesiceras* (*Ringnesiceras*) n. sp. aff. *amundense* is available, it is described in open nomenclature and only tentatively assigned to *Ringnesiceras* in spite of the fact that it is evidently a most important form. This specimen appears to be very closely allied to *R.* (*R.*) *amundense* because of its wide umbilicus and similar sculpture. Should the above interpretation of its early scultpure be confirmed from additional material, the species to which our specimen belongs would probably have to be interpreted as the rootstock of the *Ringnesiceras* lineage.

Affinities and differences. Specimen is similar to *R.* (*R.*) *amundense* in many respects, especially in the shape and arrangement of its primary ribs or bullae. However, the latter form is considerably broader-whorled and appears to be restricted to the considerably younger bed 5.

It differs from *R.* (*R.*) *pseudopolyptychum* especially in a broader and funnel-like umbilicus, the radially oriented extensions of primary ribs and a shorter growth stage provided with *Simbirskites*-like primary ribs.

Stratigraphic relationships and age. The only representative of ?*Ringnesiceras* (*Ringnesiceras*) n. sp. aff. *amundense* is derived from the level of fossiliferous beds 7-9 of the upper Deer Bay Formation (Kemper, 1977, Figure 3; Kemper and Jeletzky, 1979, p. 13, Figure 1). It is derived accordingly either from the uppermost lower Valanginian or from the lower/upper Valanginian transition beds.

Ringnesiceras (*Elleficeras*) Kemper and Jeletzky 1979

Type species. *Ringnesiceras* (*Elleficeras*) *ellefense* Kemper and Jeletzky 1979.

Origin of name. From the occurrence of the type species on Ellef Ringnes Island of Sverdrup Archipelago, N.W.T.

Diagnosis. A subgenus of *Ringnesiceras* characterized by slender and high, discus-like shaped whorls, except for the early juvenile growth stages, and a narrow umbilicus. The generally speaking *Dichotomites*- or *Homolsomites*-like ribbing habit includes fine simbirskitiform primary ribs and tubercles in late juvenile and early intermediate growth stages. The generally *Prodichotomites*-like early adult external suture line has four auxiliary lobes.

Remarks. Like the subgenus *Ringnesiceras* sensu stricto, the subgenus *Elleficeras* is characterized by a simbirskitiform development of primary ribs in the late juvenile and early intermediate growth stages. No polyptychitid umbilical bullae occur in these growth stages. Instead we observe adumbilically extended primary ribs with their tubercle-like greatest elevations not near the umbilical shoulders but appreciably farther adventrally. These primary ribs extend directly into one of the secondary ribs. Other secondaries split off from them whenever they are not intercalated between the rib bundles. The point of subdivision of primary ribs is situated on the lower flank at an appreciable distance from the umbilical shoulder.

In spite of the fact that not all of these primary ribs have a simbirskitiform tubercle near their subidivision into secondary ribs, they differ fundamentally from those of the genera *Polyptychites*, *Dichotomites*, *Prodichotomites* and *Astieriptychites*. These genera posses umbilical bullae in all late juvenile to adult growth stages, including those equivalent to the growth stages where simbirskitiform ribs and tubercles occur in *Elleficeras*. These bullae, which tend to be more or less comma-shaped, are superimposed on the ventral shoulder and the secondary ribs arise directly out of them.

A diametrically opposed development occurs in the superficially similar *Homolsomites* ex gr. *quatsinoensis* (see Jeletzky, 1965a, Pl. XX, figs. 2-7, 13-15) in which neither bullae nor simbirskitiform primary ribs are present. The fine and low primary ribs of these *Homolsomites* bifurcate or subdivide irregularly rather high on the flank. In the advanced growth stages these ribs commonly subdivide above the middle of the flank. In combination with the greater number of auxiliary lobes and the markedly ascendant orientation of the external suture line (compare Jeletzky, 1979, Figure 1U), these sculptural differences assert that *Homolsomites* is a craspeditid homeomorph of *Elleficeras*.

The suture line of *Elleficeras* (Figure 61e) differs less from that of the superficially similar *Prodichotomites*, as for example *Prodichotomites perovalis* (Koenen) (Figures 44a, 44b), than it does from that of *Homolsomites*. *Elleficeras* has only four auxiliary lobes and its external suture line is suspensive rather than ascendant and so rather like that of *Prodichotomites*. However, the sculptural development of the two is radically different. In spite of the fact that the diagnostic features of *Elleficeras* only become evident by thorough study, it obviously is a close ally of *Ringnesiceras* which is only superficially similar to some *Prodichotomites* and *Homolsomites*. As already mentioned in the description of *Ringnesiceras*, *Elleficeras* appears to be an offshoot of its principal lineage designated herein as subgenus *Ringnesiceras* sensu stricto (Fig. 11). *Elleficeras* is accordingly considered to be but a subgenus of *Ringnesiceras*.

The subgenus *Elleficeras* is so far only known from the upper Deer Bay Formation of Sverdrup Basin. However, it may occur in Valanginian rocks of the Pechora Basin in Central Russia. In spite of their superficial similarity to *Dichotomites* or *Homolsomites*, "*Olcostephanus*" *petschorensis* Bogoslovsky and "*O.*" cf. *bidichotomus* Bogoslovsky, which are two of the most commonly cited late Valanginian forms of that region, seem to be *Elleficeras*. These two species are consistently placed into *Dichotomites* in the Russian (e.g. Saks et al., 1965; Saks and Shulgina, 1974; Shulgina, 1978) and West European (e.g. Frebold, 1929) literature since the erection of that generic name by Koenen (1909). Jeletzky (1973, p. 73) concluded that "*O.*" *petschorensis* is a *Homolsomites* ex gr. *H. quatsinoensis* (Whiteaves) because of the presence of at least four auxiliary lobes in its advanced external suture line. However, because of the shape and proportions of intermediate and early whorls of the ammonites assigned to "*Olcostephanus*" *petschorensis* and "*O.*" cf. *petschorensis* by Bogoslovsky (1902, Pl. XII, figs. 1-4), they could well belong to *Elleficeras* ex aff. *E. ellefense*. Unfortunately, none of these specimens exhibits simbirskitiform primary ribs and bullae diagnostic of this genus. Furthermore, the fine primary ribs of smaller specimens (e.g. Bogoslovsky, 1902, Pl. XII, figs. 2a, 3a, 4a) tend to bifurcate or to subdivide irregularly higher upflank than those of *Elleficeras ellefense*. In view of these apparent morphological distinctions of "*O.*" *petschorensis* and "*O.*" cf. *petschorensis* from the Canadian *Elleficeras* and because of unavailability of any comparative material of these forms, the writers feel unable to determine them generically. These forms represent homoeomorphs that were arising in *Prodichotomites*, *Homolsomites* and *Elleficeras* and can only be definitely determined generically when they are represented by a more numerous material.

"*Olcostephanus*" cf. *bidichotomus* of Bogoslovsky (1902, Pl. 13, fig. 1a-1c) is a much more *Elleficeras ellefense*-like form in regard to the above critical morphological features. However, it may be a *Prodichotomites* in spite of that.

The probable presence of the subgenus *Elleficeras* in the upper Valanginian of European Russia (Pechora Basin) suggests that this presumably endemic Canadian subgenus has an extensive geographical range and so is an important interregional index fossil of the equivalents of *Ringnesiceras* (*Ringnesiceras*) *pseudopolyptychum*-Beds.

Ringnesiceras (*Elleficeras*) *ellefense* Kemper and Jeletzky 1979

Plate 60, figure 1A, 1B, 3A-3D; Figure 61e.

?1902 *Olcostephanus* cf. *bidichotomus* Bogoslovsky, p. 43-45, 131-132, Plate XIII, figures 1a-1c.

1979 *Ringnesiceras* (*Elleficeras*) *ellefense* Kemper and Jeletzky, p. 11, 12; Pl. 1, fig. 3; Pl. 2, fig. 1A, 1B, Figure 7.

Holotype. Specimen GSC 61757 originally reproduced in Plate 1, figure 3, Plate 2, figure 1a, b of Kemper and Jeletzky's (1979) paper and refigured in Pl. 60, fig. 3A-3D; Figure 61e of this paper.

Material. Two specimens (GSC 61757, 77132) from the upper Deer Bay Formation on Ellef Ringnes Island.

Locus typicus. Ellef Ringnes Island, 13 km southeast of Isachsen Weather Station; Lat. 78°43'N; Long. 103°00'W.

Stratum typicum. Upper Deer Bay Formation, basal Amundense-Beds. Upper Valanginian (see Kemper and Jeletzky, 1979, p. 13 for further details).

Diagnosis. *Elleficeras* species which differs from the only other known, informally described species (*Elleficeras* n. sp. indet.) in relatively coarser ribbing habit.

Measurements in mm.

Specimen	Shell diameter	Umbilicus	wh 1	wh 2	wth 1	wth 2
GSC Cat. No. 61757	59	15(26)	19(33)	26(44)	17	23

Description. The holotype (Pl. 60, fig. 3A-3D; Figure 61e) is a phragmocone without any trace of the body chamber. It reveals the morphology of two whorls, the adoral of which appears to be the penultimate whorl. The lesser part of the preceding third whorl is observable within the second whorl. This only partly visible third whorl is still wider than high while the other two are slender and higher than wide. The relative slenderness of the whorl increases in the course of the ontogeny. The whorl's cross-section is rounded-triangular with distinctly convex flanks (Pl. 60, fig. 3C-3D). The greatest width of the whorl occurs near the broadly rounded umbilical shoulder. Therefrom it decreases all the way upflank to the narrowly arched venter. The narrow umbilicus is shallow and its low walls are distinctly convex. However, the umbilicus is step-like rather than funnel-like as the last whorl covers only about 77 per cent of the preceding whorl.

Most of the adult (presumably early adult) external suture line is directed subradially (Figure 61e). This generally speaking *Prodichotomites*-like suture (see p. 208 for further details) has four auxiliary lobes in addition to two lateral lobes and its auxiliary part is somewhat descendant.

The second last preserved whorl is ornamented by at least twenty-two primary ribs, which begin on the outer third of the umbilical wall. These ribs are low on the umbilical shoulder and become higher further upflank. The greatest height is attained near the place where the secondaries split off (Pl. 60, fig. 3A). However, the ribs do not become markedly tuberculate even at that place, so that their overall appearance can only be defined as feebly simbirskitiform. The aptness of this definition is further stressed by the fact that the primary ribs are relatively short and extend only a small distance toward the middle of the flank. In spite of these qualifications, the presence of simbirskitiform primary ribs instead of bullae is obvious. These primaries are approximately radially oriented to the end of the second last preserved whorl. Their extensions on the umbilical wall peter out in its outer third.

The primary ribs are still simbirskitiform on the adapical part of the last preserved, presumably penultimate whorl. However, they acquire a slight comma-like bend at the umbilical shoulder in this segment. Farther adorally the primary ribs become more and more bullae-like to the oral end of the whorl. This attests that *R.* (*E.*) *ellefense* exhibits the same recurrence of umbilical bullae in the adult growth stage as in the previously described species of the subgenus *Ringnesiceras*.

The secondary and tertiary ribs are relatively coarse for the subgenus; they bend forward markedly on the venter (Pl. 60, figs. 3C, 3D). On the preserved penultimate whorl the rib bundles consist of two secondary ribs of which either both or the posterior only bifurcate again. The tertiary ribs subdivide at various levels within the adventral half of the flank. Bifurcating intercalated ribs occur between the rib bundles on the first half of the oralmost preserved whorl. Then the bundling of ribs becomes disorganized on the oralmost quarter of that whorl. This indicates an advanced age of the holotype which apparently includes most of the penultimate whorl (i.e. to the point closely before the beginning of the adult body chamber).

The second specimen placed in *R.* (*E.*) *ellefense* is a deformed fragment (Pl. 60, fig. 1A, 1B), which is larger but more narrowly umbilicate than the holotype. This paratype is also entirely septate and so does not permit any definitive conclusions concerning its adult size. Nor is it fit to provide any measurements. It is possible to see that its whorls become relatively more slender in the course of the ontogeny than those of the holotype. The last preserved whorl of the paratype is again ornamented by bullae which split into three secondary ribs. These secondaries bifurcate again in the mid-zone of the flank. The subdivision points of secondary ribs are situated approximately but not exactly at the same level which results in an only approximately tridichotomous appearance of the bundles (Pl. 60, fig. 1A). There are rare instances where one secondary rib splits into three tertiary ribs. It was not possible to observe the ribbing habit of earlier whorls. This fragment is assumed to be a morphologically extreme variant of *R.* (*E.*) *ellefense* until its status is clarified through the discovery of additional, better preserved material.

Affinities and differences. The affinities and morphological differences of our species have been discussed in the description of the subgenus *Elleficeras*, which see for further details.

It is impossible to decide at present whether or not the solitary example of "*Olcostephanus*" cf. *bidichotomus* Bogoslovsky, 1902 can be placed into the synonymy of *R.* (*E.*) *ellefense*, in spite of its far-reaching similarity to the Canadian holotype in most features. This specimen of "*Olcostephanus*" cf. *bidichotomus* of Bogoslovsky (1902, Pl. 13, figs. 1a-1c) was placed in *Dichotomites* by Jeletzky (1973, p. 73) because of its polyptychitinid suture line which is suspensive in the auxiliary part and apparently has not more than three auxiliary lobes. However, the distinctly elevated primary ribs of this form are elongated and straight to almost straight (Bogoslovsky, 1902, Pl. XIII, fig. 1a) whilst the apicalmost of these ribs appear to exhibit tubercle-like elevations at the points of their subdivision. The whorl shape and sculpture of this specimen are similar to those of the Canadian holotype of *R.* (*E.*) *ellefense*. However, these features are inconclusive, the relevant figure of Bogoslovsky (1902, Pl. XIII, fig. 1a) being a line drawing (Kemper and Jeletzky, 1979, p. 13). Furthermore, as already mentioned in the description of *Elleficeras*, the genera *Dichotomites*, *Homolsomites* and *Elleficeras* develop nearly completely homoeomorph forms that can only be distinguished when numerous specimens are available.

Stratigraphic relationships and age. The Canadian representatives of *Ringnesiceras* (*Elleficeras*) *ellefense* were found in those beds of the Ellef Ringnes Island profile (i.e. Ke 76/3/-2 and -3) which appear to be correlative with the basal part of the Amundense Beds (Figure 62). This correlation is based on their association with the earliest known representatives of *Homolsomites* cf. and aff. *H. quatsinoensis* (for further details see the stratigraphical section).

Ringnesiceras (*Elleficeras*) n. sp. indet.

Pl. 60, fig. 2A-2D.

Material. One damaged specimen GSC Cat. 77133 from Ellef Ringnes Island, GSC loc. 93868 (Ke 76/3/-3).

Description. *Ringnesiceras* (*Elleficeras*) n. sp. indet. is morphologically different from *R.* (*E.*) *ellefense* Kemper and Jeletzky and is presumably new. However, it was decided to describe it in open nomenclature because of the availability of only one inferior specimen which is unsuitable to serve as its holotype. It is strongly deformed. The largest shell diameter is estimated at about 30 mm, so it is probably a juvenile shell. The height of the whorl is approximately equal to its width at the end of the last preserved whorl. The flanks are only feebly convex and subparallely oriented. The ventral region is regularly arched.

The umbilical shoulder is broadly rounded. The umbilical wall is very low and convex. The evidently only moderately narrow umbilicus is nevertheless step-like.

The suture line is not visible.

Only addorsal segments of primary ribs are visible on the penultimate preserved whorl. They are slender with knife-like sharpened tops and have a triangular cross-section. These primary elements are not elevated on the umbilical shoulder and are accordingly not bullae but primary ribs. They are radially oriented and peter out on the external quarter of the umbilical wall. The penultimate preserved whorl carries 27 of these ribs. On the last preserved whorl the ribs gradually bend with a comma-like swing forward on the umbilical shoulder. However, they do not become bullae even here, as the maximum elevation of the primary ribs is situated not on the umbilical shoulder but farther adventrally at the point where the secondary ribs split off. Therefore, these ribs are simbirskitiform, even if they are not strictly radially oriented.

The rib bundles on the early half of the last whorl are trivirgatitpartitous. Only the posterior rib of their two secondaries splits in two. Then, on the oral part of the whorl the anterior secondary rib of the bundles begins to bifurcate increasingly frequently.

Affinities and differences. This specimen differs from the allied species *R.* (*E.*) *ellefense* in its more delicate and more dense sculpture.

Stratigraphic relationships and age. The only representative of *Ringnesiceras* (*Elleficeras*) n. sp. indet. was found in the upper Deer Bay Formation of Ellef Ringnes Island in the middle part of the upper Valanginian beds. These beds presumably correspond to the *Ringnesiceras* (*Ringnesiceras*) *pseudopolyptychum* Beds of Amund Ringnes Island (*see* Figure 62 and Kemper and Jeletzky, 1979, p. 13, Figures 1, 9 for further details).

BIOSTRATIGRAPHY

Biostratigraphy of the Valanginian and its South to North correlation.

The stratotype and the interpretation of the Tethyan facies of the Valanginian.

The Valanginian was erected by Desor in 1854. The stratotype is situated in the Seyon ravine near the village of Valangin and not far from Neuchâtel in the Jura Mountains of Switzerland. A review of the historical development of the concept of this stage was recently published by Rawson (1983). The reader is referred to this publication for further details. The stratotype is situated near the northern margin of the Tethyan Realm and represents its extremely poorly fossiliferous, marginal marine facies. Therefore, the stratotype does not permit either any reliable long range correlations of its rocks or any meaningful biostratigraphical definitions of the stage boundaries. Because of the inadequacy of the stratotype, the early workers (particularly Kilian in several papers) have worked out the critical aspects of the concept of the Valanginian Stage in sections situated in the Southeast France. In the region of the French Alps the Valanginian is thick, rich in fossils and excellently exposed in many areas of the Vocontian Trough. This has finally led the French stratigraphers to the formal designation of the Vocontian facies as a hypostratotype of the stage. The profile of Angles with a complementary profile at Barret-le-Bas was selected as such and excellently described (Busnardo et. al., 1979). The time ranges of the most important fossil groups were worked out and summarized in tables. This work facilitated the subdivision of the hypostratotype into six zones.

The Zone of *Kilianella roubadiana* (d'Orbigny) has served for a long time as the basal zone of the stage. More recently, however, Le Hégarat and Remane (1968) have differentiated the Subzone of *Thurmanniceras pertransiens* as the lowermost member of the Valanginian. The faunal change between the Berriasian and the Valanginian was considered to be abrupt. However, Busnardo and Thieuloy (in Busnardo et al., 1979) discovered that a mixture of Berriasian and Valanginian faunal elements occurs in the basal part of the Pertransiens Zone of Le Hégarat (in Le Hégarat and Remane, 1968). They have accordingly erected a new unit the zone of *Thurmanniceras otopeta* Thieuloy — for the lowermost part of the Pertransiens Subzone.

Still more recently Hoedemaker (1982) proposed a new subzone, that of *Tirnovella alpillensis*, based on his observations in Southeast Spain. This subzone was inferred to be correlative with the Callisto-Subzone of Le Hégarat and Remane (1968). However, while the French Callisto-Subzone contains only Berriasian ammonites and so is the topmost subzone of this stage, its Spanish counterpart contains already some Valanginian ammonites. Hoedemaker (1982) has, accordingly, treated the Alpillensis-Subzone as the basal Valanginian unit.

The results of Hoedemaker demonstrate conclusively the kinds of problems caused by the practice of drawing stage boundaries according to a Berriasian or Valanginian "character" of some of their ammonites. In this particular case, *Kilianella* forms are considered to be Valanginian ammonites. These results show, furthermore, that many groups of Neocomitinae are restricted to particular regions and so have hardly an interregional value. This last point is particularly weighty as it demonstrates that from the standpoint of stratigraphers working in the Boreal Realm an Otopeta- or Alpillensis-Zone can under no circumstances be recognized as the basal unit of the Valanginian. It is regrettable that Busnardo and Thieuloy (in Busnardo et al., 1979) have completely disregarded Kemper's (1971) proposal to use the first appearance of *Platylenticeras* as the event defining the lower boundary of the Valanginian. This proposal is particularly important from the above standpoint as *Platylenticeras* can be used to effect a North-South correlation of this boundary over broad expanses of Europe (see Kemper, 1971 for further details). In southeastern France the first *Platylenticeras* appear at the base of the Pertransiens-Zone in the sense of Busnardo et al. (1979). The Otopeta-Zone must be treated as the topmost Berriasian from that standpoint (Figure 62).

In the Tethyan Realm the lower/upper Valanginian boundary is defined by the first appearance of *Saynoceras verrucosum*, which is also present in the southern marginal belt of the Boreal Realm (Figure 62).

Acanthodiscus radiatus was considered from early times as an index fossil of the basal Hauterivian in the Tethyan Realm. It was recently confirmed in that role by Busnardo et al. (1979). *A. radiatus* has, however, an important defect as in index fossil. It is restricted predominantly to the shallow water facies margining various basins while being either absent or very rare in their central parts. On the other hand it has the advantage of being present in the southern part of the Boreal Realm (i.e. in Northwest Germany; Figure 62) as well as in Tethys.

Acanthodiscus radiatus is so rare in the Boreal Realm (and evidently in the central part of the Vocontian Trough of Southeast France as well) that it is hardly of any everyday practical use for the purpose of definition of the

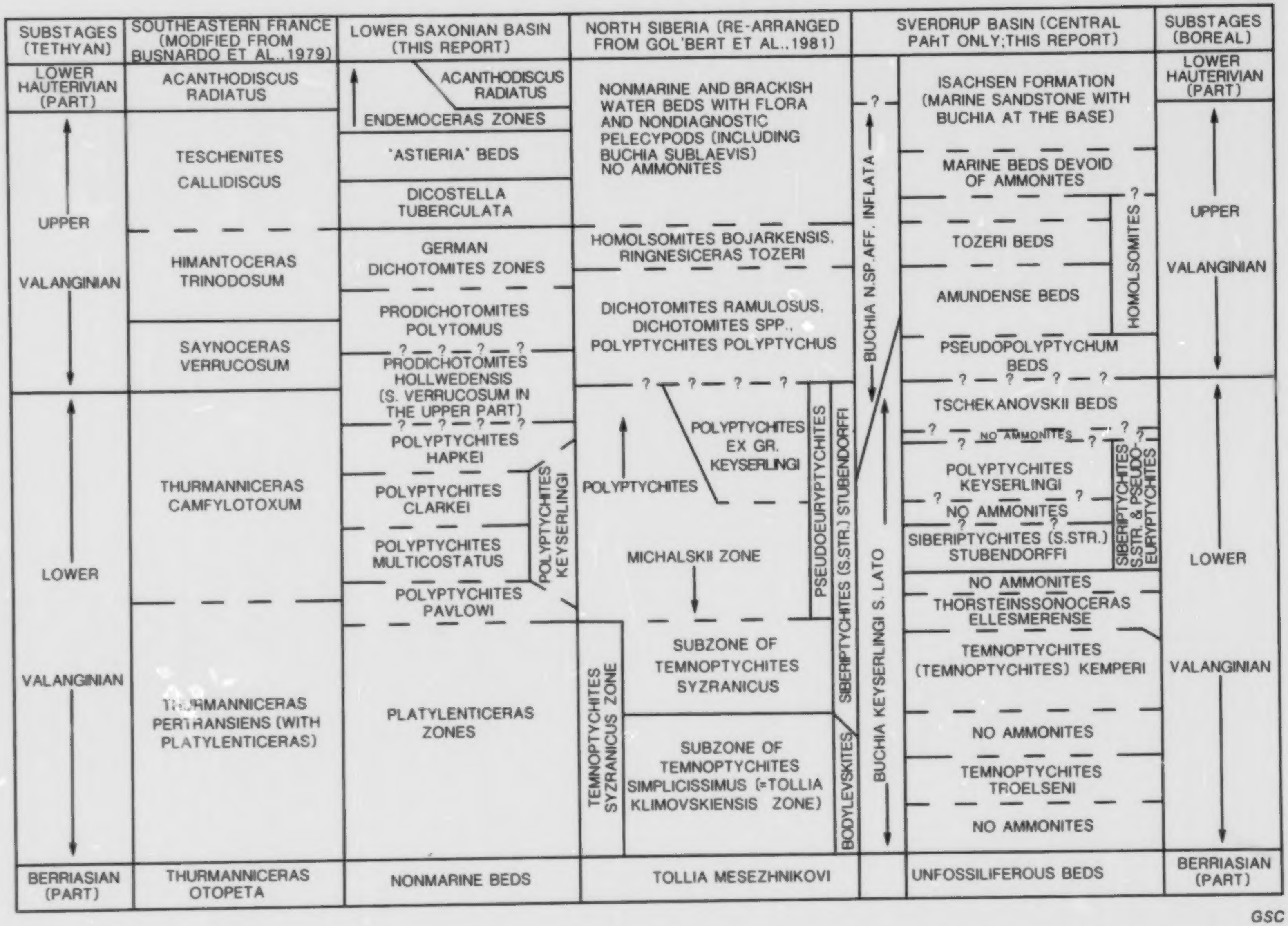

SUBSTAGES (TETHYAN)
LOWER HAUTERIVIAN (PART)
UPPER
VALANGINIAN
LOWER
VALANGINIAN
BERRIASIAN (PART)
SOUTHEASTERN FRANCE (MODIFIED FROM BUSNARDO ET AL., 1979)
ACANTHODISCUS RADIATUS
TESCHENITES CALLIDISCUS
HIMANTOCERAS TRINODOSUM
SAYNOCERAS VERRUCOSUM
THURMANNICERAS CAMFYLOTOXUM
THURMANNICERAS PERTRANSIENS (WITH PLATYLENTICERAS)
THURMANNICERAS OTOPETA
LOWER SAXONIAN BASIN (THIS REPORT)
ACANTHODISCUS RADIATUS
ENDEMOCERAS ZONES
'ASTIERIA' BEDS
DICOSTELLA TUBERCULATA
GERMAN DICHOTOMITES ZONES
PRODICHOTOMITES POLYTOMUS
? — ? — ? — ?
PRODICHOTOMITES HOLLWEDENSIS (S. VERRUCOSUM IN THE UPPER PART)
? — ? — ? — ?
POLYPTYCHITES HAPKEI
POLYPTYCHITES CLARKEI
POLYPTYCHITES MULTICOSTATUS
POLYPTYCHITES PAVLOWI
POLYPTYCHITES KEYSERLINGI
PLATYLENTICERAS ZONES
NONMARINE BEDS
NORTH SIBERIA (RE-ARRANGED FROM GOL'BERT ET AL., 1981)
NONMARINE AND BRACKISH WATER BEDS WITH FLORA AND NONDIAGNOSTIC PELECYPODS (INCLUDING BUCHIA SUBLAEVIS) NO AMMONITES
HOMOLSOMITES BOJARKENSIS, RINGNESICERAS TOZERI
DICHOTOMITES RAMULOSUS, DICHOTOMITES SPP., POLYPTYCHITES POLYPTYCHUS
? — ? — ? — ?
POLYPTYCHITES EX GR. KEYSERLINGI
POLYPTYCHITES
MICHALSKII ZONE
PSEUDOEURYPTYCHITES
SIBERIPTYCHITES (S.STR.) STUBENDORFFI
SUBZONE OF TEMNOPTYCHITES SYZRANICUS
SUBZONE OF TEMNOPTYCHITES SIMPLICISSIMUS (=TOLLIA KLIMOVSKIENSIS ZONE)
TEMNOPTYCHITES SYZRANICUS ZONE
BODYLEVSKITES
TOLLIA MESEZHNIKOVI
?
BUCHIA N.SP.AFF. INFLATA
BUCHIA KEYSERLINGI S. LATO
SVERDRUP BASIN (CENTRAL PART ONLY; THIS REPORT)
ISACHSEN FORMATION (MARINE SANDSTONE WITH BUCHIA AT THE BASE)
MARINE BEDS DEVOID OF AMMONITES
?
TOZERI BEDS
AMUNDENSE BEDS
HOMOLSOMITES
PSEUDOPOLYPTYCHUM BEDS
? — ? — ? — ?
TSCHEKANOVSKII BEDS
? NO AMMONITES ? ?
POLYPTYCHITES KEYSERLINGI
? ?
NO AMMONITES
? ?
SIBERIPTYCHITES (S.STR.) STUBENDORFFI
SIBERIPTYCHITES S.STR. & PSEUDO-EURYPTYCHITES
NO AMMONITES
THORSTEINSSONOCERAS ELLESMERENSE
TEMNOPTYCHITES (TEMNOPTYCHITES) KEMPERI
NO AMMONITES
TEMNOPTYCHITES TROELSENI
NO AMMONITES
UNFOSSILIFEROUS BEDS
SUBSTAGES (BOREAL)
LOWER HAUTERIVIAN (PART)
UPPER
VALANGINIAN
LOWER
VALANGINIAN
BERRIASIAN (PART)
GSC

Figure 62. Sequence of Valanginian ammonite faunas of Sverdrup Basin and their correlation with those of Northern Siberia, Lower Saxony Basin and the Vocontian Trough of Southeast France.

Valanginian-Hauterivian boundary. Therefore, this definition of the boundary cannot be achieved satisfactorily even within the Tethyan Realm proper where other criteria are needed. It should be mentioned in this connection that there are other late late Valanginian ammonite genera (e.g. *Dicostella*) that occur in both realms (Figure 62). It is possible to use them instead of *A. radiatus* for correlation.

Because of the above considerations, the definition of the Valanginian proposed by Busnardo et al. (1979) cannot be recognized as valid. It is instead but one of a number of possible propositions until the Cretaceous Subcommittee of IUGS produces a binding decision about the lower and upper boundaries. The definition favored by the writers is presented in Figure 62.

The significance of the Lower Saxony Basin for South-North correlation.

The Lower Saxony Basin formed a southern marginal sea of the Cretaceous North Sea. Both of them formed the southern part of the Boreal Realm, the marine faunas of which differed fundamentally from those of the Tethyan Realm. The North Sea and its marginal basins were paleobiogeographically important because they were connected by seaways with adjacent Tethyan basins. Therefore, migrating Tethyan ammonites did penetrate into them and existed there alongside the prevalent endemic groups of fossils. The North Sea formed, therefore, an overlap area of these two paleozoogeographical realms and was ideally suited to facilitate the interrealm correlations (see Rawson and Kemper, 1978; Kemper et al., 1981). The recognition of this fact forms the basis of the biostratigraphical part of this project, that aims to correlate the Valanginian of the high Boreal Sverdrup Basin with that of the marginal Tethyan type-area using the sequence of mixed Valanginian faunas of Lower Saxony basin.

It is a happy accident that the previously mentioned Tethyan genera and species, that were either used for the definition of the Valanginian stage and its substages by the French workers or could have been used by them, also occur in the southern Boreal basins of Northwest Germany. It is this paleozoogeographical accident that permits us to project in an optimal way the positions of the lower and lower/upper Valanginian boundaries from Southeast France into that particular basin of the Boreal Realm that was the principal evolutionary center of Polyptychitinae (see Kemper et al., 1981; this paper p. 6, 7, Figure 11). In the Lower Saxony Basin the lower boundary is marked by the appearance of *Platylenticeras* while the base of the upper Valanginian is defined by the appearance of *Saynoceras verrucosum* (Figure 62).

In Northwest and Middle Europe the Valanginian/Hauterivian boundary is not defined by the appearance of *Acanthodiscus radiatus*. Instead it is placed where the genus *Endemoceras* appears for the first time (Figure 62), which maybe slightly earlier. So far there is no agreement among specialists about the validity of this boundary, which remains problematic and unsatisfactory in the authors' opinion.

As can be seen in Figure 11 of this paper, the evolutionary development of Polyptychitinae in the Lower Saxony Basin exhibits two principal phases, one in the early early Valanginian and another at the early/late Valanginian boundary. This development is important as it permits the recognition of these levels as originally defined in Northwest Germany elsewhere in the southern Belt of the Boreal Realm using the Polyptychitinae taxa.

In addition to using *Platylenticeras*, the lower lower Valanginian of the southern part of the Boreal Realm can also be defined by the presence of *Paratollia* and *Bodylevskites*. The basal upper Valanginian of that belt can also be defined by the first appearance of *Prodichotomites* and *Dichotomites*. In Northwest Germany Polyptychitinae disappear well before the end of the Valanginian. Therefore, it is necessary to use Thethyan immigrant ammonites for the subdivision of the latest Valanginian of that region (Kemper et al., 1981).

Subdivision and delimitation of the Valanginian in the Sverdrup Basin.

The Valanginian biostratigraphy of the Sverdrup Basin was already comprehensively discussed by Jeletzky (1973, 1979) and Kemper and Jeletzky (1979). Kemper (1975, 1977, Figure 3) has, furthermore, published detailed descriptions of the two most important Valanginian profiles he has measured there and dated their principal ammonite faunas in terms of North Siberian and Lower Saxony ammonite zones. These biostratigraphical data are still valid for the most part and the reader is referred to the above publications for further details. However, for the reader's convenience the presently known sequence of Valanginian ammonite faunas of the Sverdrup Basin and their correlation with the Valanginian ammonite zones of Northern Siberia, the Lower Saxony Basin, and the Vocontian Trough of Southeast France are summarized in Figure 62. Further biostratigraphical details, including the updating of some outdated conclusions, are provided in the preceding descriptions of the Sverdrup and Lower Saxony Polyptychitinae and Simbirskitinae taxa.

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FOSSIL LOCALITIES IN SVERDRUP BASIN

GSC loc. 24024: *Siberiptychites* (*Siberiptychites*) *fascicostatus* n. sp.

Upper Deer Bay Formation, exact level and age uncertain but the specimen is believed to be derived from the lower part of *Siberiptychites*-Beds equivalent to GSC loc. 37867 and beds 16, 17 of Section Ke 74/11; ?mid lower Valanginian. Ellef Ringnes Island, N.W.T.; 3 miles north of Salt Dome; Lat. 78°30'N, Long. 109°00'W.

GSC loc. 37867: *Siberiptychites* (*Siberiptychites*) *stubendorffi* (Schmidt 1872); *S.* (*Pseudoeuryptychites*) *middendorfi* (Pavlow 1914) var. *incrassata* (Pavlow 1914); *S.* (*S.*) *fascicostatus* n. sp.

Upper Deer Bay Formation; collected from a concretion lying loose on the surface; exact stratigraphic position within the formation is unknown but it is assumed to be 91 m to 106 m stratigraphically below GSC loc. 100800 that has yielded *Homolsomites* aff. *quatsinoensis* and *Ringnesiceras tozeri*. The association of the holotype of *S.* (*S.*) *fascicostatus* with *S.* (*S.*) *stubendorffi* (Pl. 39, fig. 1) and *S.* (*Pseudoeuryptychites*) *middendorffi* var. *incrassata* (Pl. 39, fig. 3) indicates that GSC loc. 37867 represents beds equivalent to beds 16, 17 of measured Section Ke 74/11 and corresponds to the lower part of its *Siberiptychites*-Beds; middle part of lower Valanginian. Ellef Ringnes Island, N.W.T.; Lat. 78°30'N, Long. 104°00'W; about 1 7/8 miles east of Isachsen Weather Station on the north bank of the delta of a nameless creek slightly less than 1/2 mile from its mouth and less than 15 m above sea level.

GSC loc. 82695: *Siberiptychites* n. sp. aff. *stubendorffi* (Schmidt, 1872); *Polyptychites keyserlingi* (Neumayr and Uhlig, 1881); *Polyptychites* aff. *hapkei* n. sp.; *Polyptychites* aff. *tschekanovskii* (Pavlow, 1914), and *Polyptychites canadensis* (Kemper and Jeletzky, 1979).

Upper Deer Bay Formation, exact level and age unknown but the locality is inferred to represent the equivalents of the *Siberiptychites* n. sp. aff. *stubendorffi* and *Pseudoeuryptychites* bearing beds Ke 74/15-Ke 74/14 and the *Polyptychites tschekanovskii*-bearing Beds Ke 74/8, Ke 74/9 (Kemper, 1977, p. 3, Fig. 3). Late and ?latest early Valanginian. Collected near the northern tip of Amund Ringnes Island, N.W.T., on the north side of a large diapir; Lat. 74°40'N, Long. 98°00'W.

GSC loc. 85023: *Prodichotomites* aff. *P. hollwedensis* Kemper 1978.

Upper Deer Bay Formation, Section AK-1-150, 45 m level; Amund Ringnes Island, N.W.T.; Lat. 78°38'N, Long. 97°50'W. Collected by the Mobil Oil Co. of Canada Ltd., 1969. No further locality data available but the specimen is believed to have been collected from the equivalents of Beds 7-9 of Kemper (1977, p. 3, Fig. 3) and to represent either the topmost lower or the basal upper Valanginian.

GSC loc. 85025: *Polyptychites canadensis* (Kemper and Jeletzky, 1979); *Polyptychites balkwilli* n. sp.

Upper Deer Bay Formation, Section AK-7-490, 490-foot level. Amund Ringnes Island, N.W.T.; Lat. 78°38'N, Long. 97°50'W. Collected by the Mobil Oil Co. of Canada Ltd., 1969. No further locality data is available but the specimen is believed to have been collected from the equivalents of Beds 7-9 of Kemper (1977, p. 3, Fig. 3) and to represent either the same or slightly younger beds as GSC loc. 85023.

GSC loc. 85059: *Amundiptychites* aff. *sverdrupi* (Kemper and Jeletzky, 1979).

Upper Deer Bay Formation; exact horizon is unknown but the specimen is presumably derived from the Tschekanovskii- to Pseudopolyptychum-Beds, topmost lower to basal upper Valanginian; Northern Amund Ringnes Island, within the Airphoto A 16748-48(1); Collected by the Mobil Oil Co. of Canada Ltd., 1969.

GSC loc. 91297: *Ringnesiceras tozeri* (Kemper and Jeletzky, 1979).

Upper Deer Bay Formation, Section Ke 74/11 (Kemper, 1977, p. 3, Fig. 3), Bed -2 situated about 68 m stratigraphically below the assigned base of Isachsen Formation. Tozeri-Beds, upper Valanginian. Northwestern Amund Ringnes Island, N.W.T.; Lat. 78°32'20"N, Long. 97°56'W.

GSC loc. 91301: *Polyptychites* n. sp. A

Upper Deer Bay Formation, Section Ke 74/11 (Kemper, 1977, p. 3, Fig. 3), Bed -7 situated about 124 m to 125 m stratigraphically below the assigned base of Isachsen Formation; basal part of *Ringnesiceras pseudopolyptychum*-Beds, basal upper Valanginian. North Amund Ringnes Island, N.W.T.; Lat. 78°38'20"N, Long. 97°56'W.

GSC loc. 91302: *Polyptychites tschekanovskii* (Pavlow, 1914); *Polyptychites balkwilli* n. sp.

Upper Deer Bay Formation, Section Ke 74/11 (Kemper, 1977, p. 3, Fig. 3), Bed -8 situated about 128 m to 129 m stratigraphically below the assigned base of Isachsen Formation; *Polyptychites tschekanovskii*-Beds; ?topmost lower Valanginian, North Amund Ringnes Island, N.W.T.; Lat. 78°38'20"N, Long. 97°56'W.

GSC loc. 91303: *Amundiptychites sverdrupi* (Kemper and Jeletzky, 1979)

Upper Deer Bay Formation, Section Ke 74/11 (Kemper, 1977, p. 3, Fig. 3), Bed -9 situated 131 m to 132 m stratigraphically below the assigned base of the Isachsen Formation; *Polyptychites tschekanovskii*-Beds; ?topmost lower Valanginian. North Amund Ringnes Island, N.W.T.; Lat. 78°38'20"N, Long. 97°56'W.

GSC loc. 91308: *Siberiptychites* (*Siberiptychites*) n. sp. aff. *stubendorffi* (Schmidt, 1872).

Upper Deer Bay Formation, Bed-14 situated about 225 m stratigraphically below the assigned base of Isachsen Formation and about 24 m stratigraphically above the Bed -16 that has yielded the youngest representative of *S.* (*S.*) *stubendorffi*; upper part of *Siberiptychites*-Beds, middle part of lower Valanginian. North Amund Ringnes Island, N.W.T.; Lat. 87°38'26"N, Long. 97°54'W.

GSC loc. 91309: *Siberiptychites* (*Pseudoeuryptychites*) *pateraeformis* (Voronets, 1962).

Upper Deer Bay Formation, Section Ke 74/11 (Kemper, 1977, p. 3, Fig. 3), concretionary Bed -15 situated between 200 m and 225 m stratigraphically below the assigned base of Isachsen Formation; upper part of *Siberiptychites*-Beds, middle part of lower Valanginian. North Amund Ringnes Island, N.W.T.; Lat. 78°38'26"N, Long. 97°54'W.

GSC loc. 91310: *Siberiptychites* (*Siberiptychites*) *stubendorffi* (Schmidt, 1872); *S.* (*Pseudoeuryptychites*) *middendorffi* (Pavlow 1914); *Siberiptychites*? (subgenus novum?) sp. nov. B.

Upper Deer Bay Formation, Section Ke 74/11 (Kemper, 1977, p. 3, Fig. 3), Bed -16 situated about 249 m stratigraphically below the assigned base of Isachsen Formation; lower part of *Siberiptychites*-Beds, middle part of the lower Valanginian. North Amund Ringnes Island, N.W.T.; Lat. 78°38'26"N, Long. 97°54'W.

GSC loc. 91311: *Siberiptychites* (*Siberiptychites*) *stubendorffi* (Schmidt, 1872); *S.* (*Pseudoeuryptychites*) cf. or aff. *middendorffi* (Pavlow, 1914).

Upper Deer Bay Formation, Section Ke 74/11 (Kemper, 1977, p. 3, Fig. 3), Bed -17 situated slightly below the Bed -16, which is about 249 m stratigraphically below the assigned base of Isachsen Formation; lowermost part of *Siberiptychites*-Beds, middle part of lower Valanginian. North Amund Ringnes Island, N.W.T.; Lat. 78°38'26"N, Long. 97°54'W.

GSC loc. 91354: *Siberiptychites* (*Siberiptychites*) *stubendorffi* (Schmidt, 1872); *Astieriptychites* sp. indet. A.

Upper Deer Bay Formation, Section Ke 74/2, bed 2 that is apparently situated only about 60 m stratigraphically below the base of Isachsen Formation; some part of *Siberiptychites*-Beds and of a mid-early Valanginian age. On the float in the bed of Reptile Creek at a point 1.5 miles north from the airport of Eureka Weather Station, Ellesmere Island, N.W.T.; approximate Lat. 80°00'18"N, Long. 85°25'W.

GSC loc. 91376: *Astieriptychites*? sp. indet. B.

Upper Deer Bay Formation, 60 m stratigraphically below the base of Isachsen Formation though it could possibly have been dropped down from a level about 10 m higher; some part of the *Siberiptychites*-Beds, of a mid-early Valanginian age. Collected on the float in the bed of Reptile Creek at a point 1.5 miles north from the airport of Eureka Weather Station, Ellesmere Island, N.W.T.; approximate Lat. 80°00'18"N, Long. 85°25'W.

GSC loc. 93753: *Amundiptychites sverdrupi* (Kemper and Jeletzky, 1979); ?*Ringnesiceras* (*Ringnesiceras*) n. sp. aff. *R.* (*R.*) *amundense* (Kemper and Jeletzky, 1979); *Amundiptychites fasciatus* n. sp.; *Amundiptychites thorsteinssoni* n. sp.

Upper Deer Bay Formation, Section Ke 76/11 (Kemper, 1977, p. 3, Fig. 3), Beds 7-9 (undivided) situated about 125 m or 124 m to 130 m or 131 m stratigraphically below the assigned base of Isachsen Formation; Tschekanovskii- to Pseudopolyptychum-Beds, topmost lower to basal upper Valanginian. Northwestern Amund Ringnes Island, N.W.T.; Lat. 78°38'20"N, Long. 97°56'W.

GSC loc. 93754: *Siberiptychites* (*Siberiptychites*) n. sp. aff. *stubendorffi* (Schmidt, 1872); *Siberiptychites* (*Pseudoeuryptychites*) sp. indet. A.

Upper Deer Bay Formation, Section Ke 76/11 (Kemper, 1977, p. 3, Fig. 3), Bed -14 situated about 225 m stratigraphically below the assigned base of Isachsen Formation and about 24 m stratigraphically above the Bed -16 that has yielded the youngest representatives of *S.* (*S.*) *stubendorffi*; upper part of *Siberiptychites*-Beds, middle part of lower Valanginian. North Amund Ringnes Island, N.W.T.; Lat. 78°38'26"N, Long. 97°54'W.

GSC loc. 93755: *Ringnesiceras* (*Ringnesiceras*) *amundense* (Kemper and Jeletzky, 1979).

Upper Deer Bay Formation, Section Ke 76/11 (Kemper, 1977, p. 3, Fig. 3), Bed-5 situated about 99 m stratigraphically below the assigned base of Isachsen Formation; Amundense-Beds, lower upper Valanginian; North Amund Ringnes Island, N.W.T.; Lat. 78°38'20"N, Long. 97°56'W.

GSC loc. 93865: *Astieriptychites obsoletus* n. sp.

Mould Bay Formation, Upper Member, more exact stratigraphic position and age not known but this specimen is believed to be derived from beds equivalent to some part of the *Siberiptychites*-Beds and to be of mid-early Valanginian age; northern part of Mackenzie King Island, N.W.T.; Lat. 77°54'N, Long. 111°09'W.

GSC loc. 93866: *Polyptychites canadensis* (Kemper and Jeletzky, 1979)

Upper Deer Bay Formation; Tschekanovskii- to Pseudopolyptychum-Beds, topmost lower to basal upper Valanginian. Amund Ringnes Island, N.W.T.; Lat. 78°38'20"N, Long. 91°56'W.

GSC loc. 93867: *Amundiptychites fasciatus* n. sp.

Upper Deer Bay Formation, Section Ke 76/11 (Kemper, 1977, p. 3, Fig. 3), Bed-7 situated about 124 m to 125 m stratigraphically below the assigned base of Isachsen Formation; basal part of *Ringnesiceras pseudopolyptychum*-Beds, basal upper Valanginian. North Amund Ringnes Island, N.W.T.; Lat. 78°38'20"N, Long. 97°56'W.

GSC loc. 93868: *Ringnesiceras* (*Elleficeras*) *ellefense* (Kemper and Jeletzky 1979); *Ringnesiceras* (*Elleficeras*) n. sp. indet. juven.

Upper Deer Bay Formation, Section Ke 76/3 (Kemper, 1977, p. 3, Fig. 3), Bed -3 situated about 117 m stratigraphically below the assigned base of Isachsen Formation; Amundense-Beds, lower upper Valanginian, 13 km southeast of Isachsen Weather Station, Ellef Ringnes Island, N.W.T.; Lat. 78°43'N, Long. 103°00'W.

GSC loc. 93870: *Ringnesiceras* (*Ringnesiceras*) *pseudopolyptychum* (Kemper and Jeletzky, 1979).

Upper Deer Bay Formation, Section Ke 76/3 (Kemper, 1977, p. 3, Fig. 3), Bed -2 situated about 116 m stratigraphically below the assigned base of Isachsen Formation; Amundense-Beds, lower upper Valanginian, 13 km southeast of Isachsen Weather Station, Ellef Ringnes Island, N.W.T., Lat. 78°43'N, Long. 103°00'W.

GSC loc. 93871: *Ringnesiceras* (*Ringnesiceras*) *pseudopolyptychum* (Kemper and Jeletzky, 1979).

Upper Deer Bay Formation, Section Ke 76/3 (Kemper, 1977, p. 3, Fig. 3), Bed -4 situated 118 m to 119 m stratigraphically below the assigned base of Isachsen Formation; Amundense-Beds, lower upper Valanginian, 13 km southeast of Isachsen Weather Station, Ellef Ringnes Island, N.W.T.; Lat. 78°43'N, Long. 103°00'W.

GSC loc. 100800: *Ringnesiceras tozeri* (Kemper and Jeletzky, 1979)

Upper Deer Bay Formation, exact locality unknown but this specimen was probably found within the uppermost 60 m of the formation. Ellef Ringnes Island, N.W.T.; Lat. 78°30'N, Long. 109°00'W. Presented by J.C. Sproule and Associates, Ltd., Calgary, Alberta.

GSC loc. C-4749: *Siberiptychites* (*Pseudoeuryptychites*) *middendorffi* (Pavlow, 1914), *S.* (*Siberiptychites*) n. sp. aff. *stubendorffi* (Schmidt, 1874).

Upper Deer Bay Formation, 2305-2322 feet below the top of a measured section. Equivalents of Beds 16 and 17 of the section of Ke 76/11 (Kemper, 1977, p. 3, Fig. 3). Lower part of **Siberiptychites**-Beds, N.W.T., west of Gibbs Fiord, Princess Margaret Range, Lat. 79°51'W.; Long. 90°00W. Collected by the Panarctic Oil Co., 1969.

Plate 1

Figure 1. *Neocraspedites* n. sp. aff. *semilaevis* (Koenen, 1902). Kuhn Collection, Dortmund, x 1.

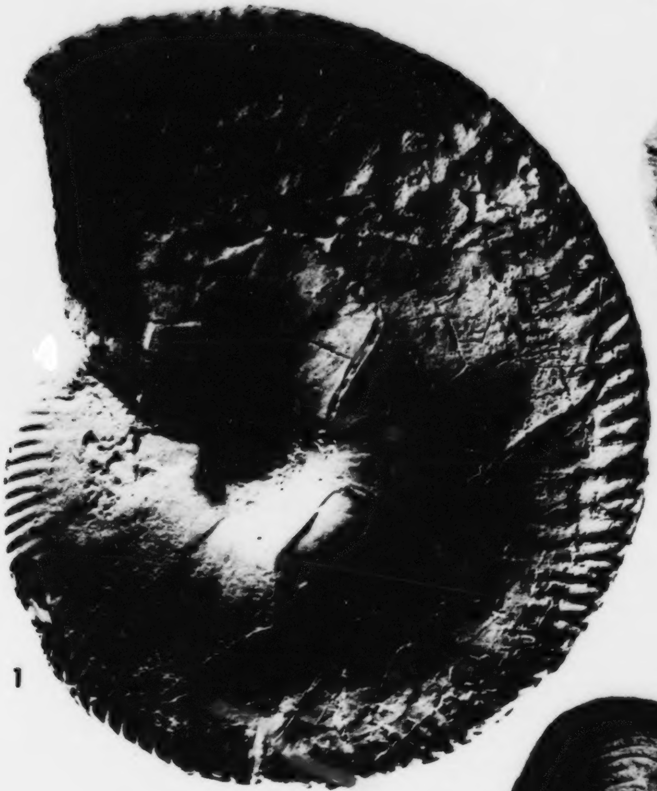
Figure 2. *Neocraspedites semilaevis* (Koenen, 1902). A thick variant, x 1.

Figure 3. *Paratollia tenuicostata* (Kemper, 1968). Holotype. BGR, kv 58, Hannover, x 1.

Figure 4A, 4B. *Paratollia tenuicostata* (Kemper, 1968). Only the living chamber is visible. Hendriksen-Collection, Hengelo, x. 1. 4A. Lateral view; 4B. Ventral view of the oral half of the whorl.

Figures 5A, 5B. *Paratollia emslandensis* (Kemper, 1964). Holotype. BGR, kv 318, Hannover. The specimen is deformed so that the umbilicus is unnaturally narrowed, x 1. 5A. Lateral view. 5B. Ventral view of the oral half of the whorl.

All specimens are from Suddendorf, Northwest Germany, upper *Platylenticeras*-Beds, lower lower Valanginian.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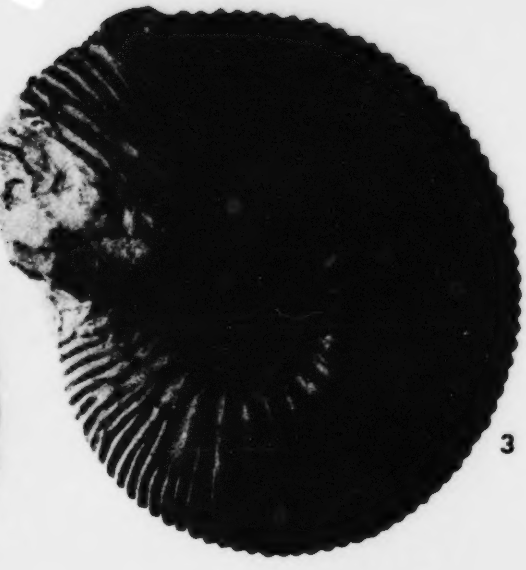
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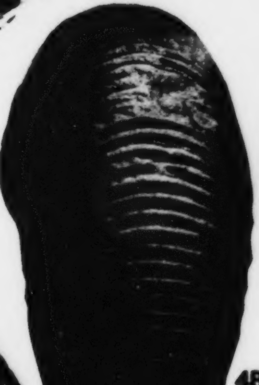
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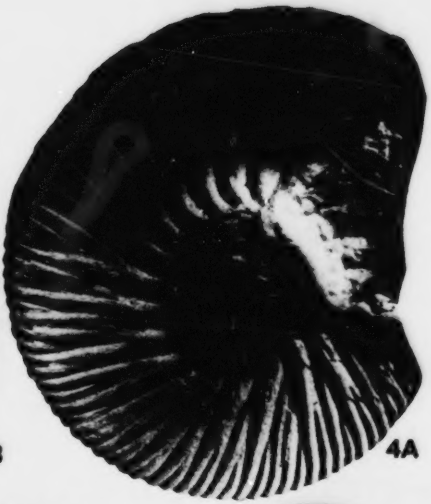
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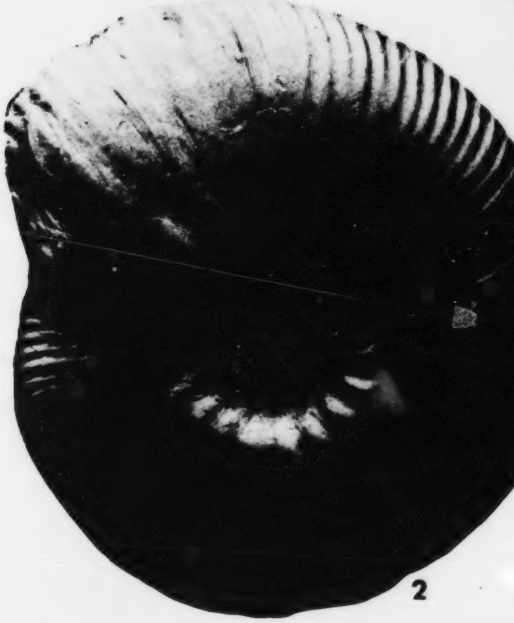
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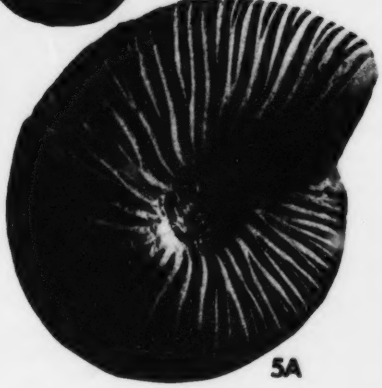
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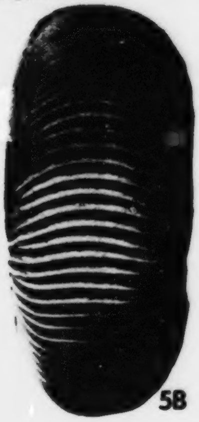
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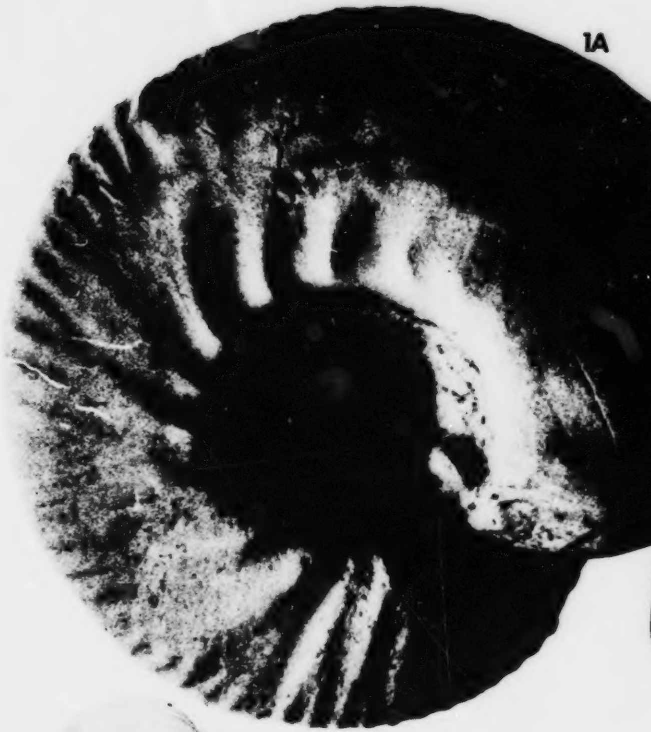
Plate 2

Figures 1A, 1B.	*Propolyptychites bentheimensis* Kemper, 1976. Upper *Platylenticeras*-Beds, lower lower Valanginian. Sachsenhagen, Northwest Germany. BGR kv 66, Hannover. A transitional form to the *Propolyptychites* ex gr. *quadrifidus*. An adult living chamber with weakened sculpture on the flanks, x 1.
Figure 2.	*Polyptychites michalskii* (Bogoslovsky, 1902). Upper *Platylenticeras*-Beds, lower lower Valanginian. Suddendorf, Northwest Germany, Plastecine impression of the internal mould of juvenile whorls. BGR, kv 261, Hannover, x 1.
Figures 3A, 3B.	*Neocraspedites semilaevis* (Koenen, 1902). Upper *Platylenticeras*-Beds, lower lower Valanginian. Sachsenhagen, Northwest Germany. BGR kv 255, Hannover. A slender, evolutionarily progressive variant that is morphologically typical of the species, x 1. 3A. Lateral view; 3B. Ventral view of the oral half of the whorl.
Figures 4A, 4B.	*Neocraspedites* n. sp. aff. *N. semilaevis* (Koenen, 1902). Upper *Platylenticeras*-Beds, lower lower Valanginian. Muesingen at Bueckeburg. Collection of the GIG. A juvenile specimen that has fine ribbing but is thick for the genus, x 1. 4A. Lateral view; 4B. Ventral view of the oral half of the whorl.



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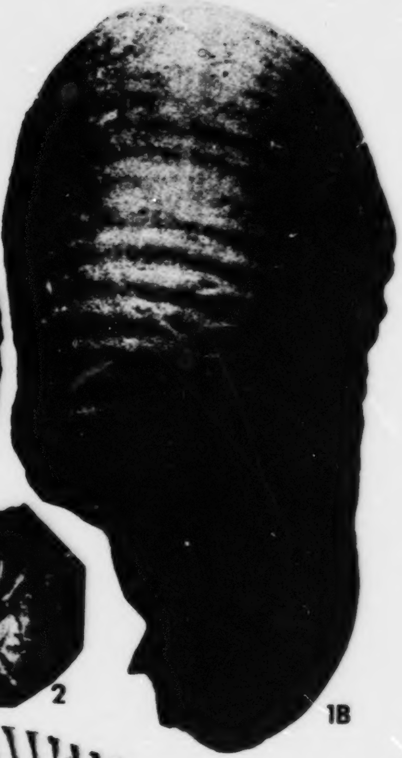

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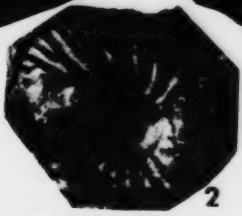

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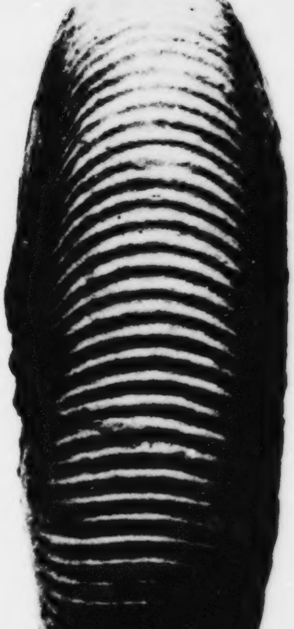

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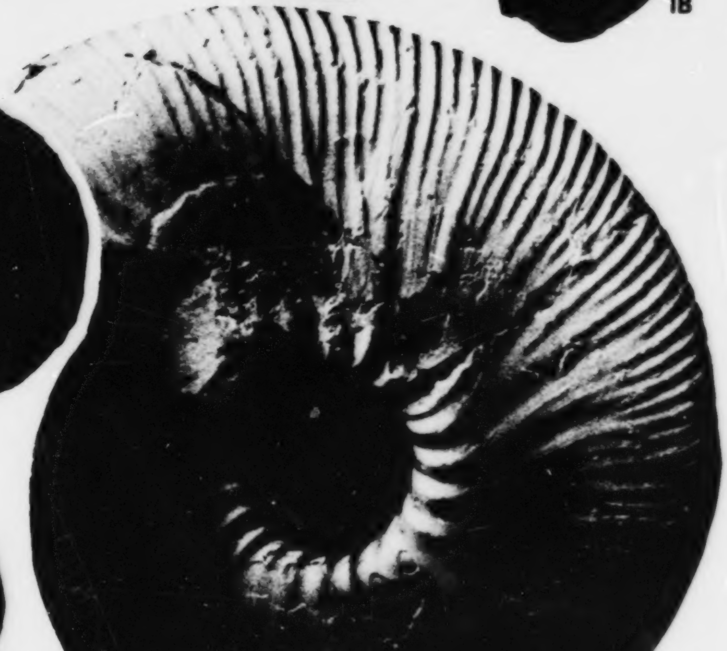

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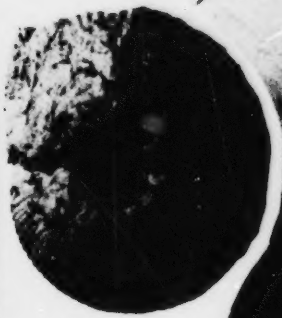

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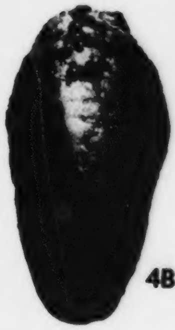

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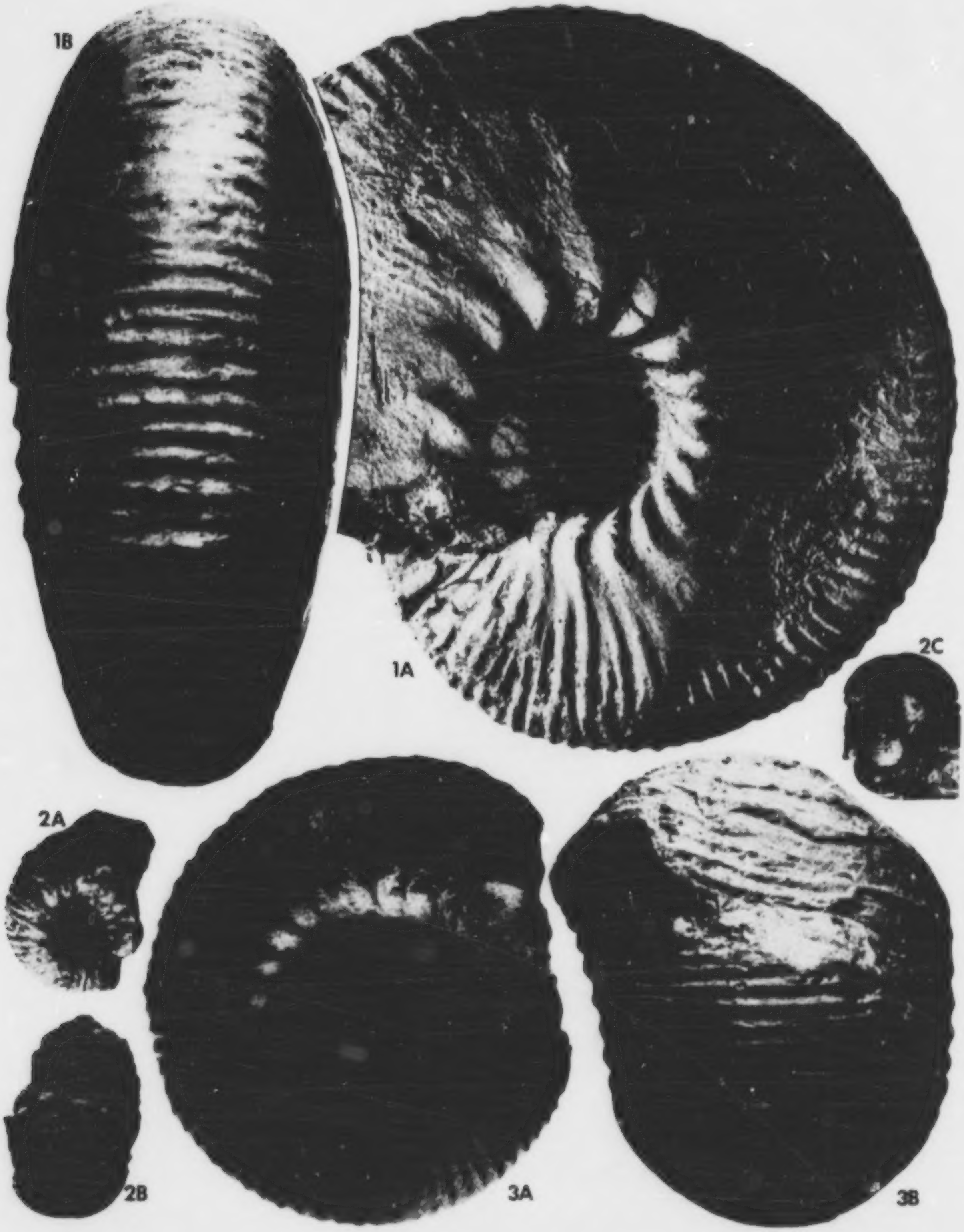
Plate 3

Figures 1A, 1B. *Neocraspedites semisulcatus* (Koenen, 1902). Upper *Platylenticeras*-Beds, lower lower Valanginian. Sachsenhagen, Northwest Germany. BGR kv 260, Hannover. Presumably the penultimate whorl and the beginning of adult living chamber, x 1. 1A. Lateral view; 1B. Ventral view of oral half of the whorl.

Figures 2A-2C. *Euryptychites latissimus* (Neumayr and Uhlig, 1881). Lower (?) *Polyptychites*-Beds, middle part of lower Valanginian. Bueckeburg-Jetenburg, Northwest Germany. BGR, kv 72, Hannover. Juvenile specimen, x 1. 2A. Lateral view; 2B. Ventral view of the oral half of the last whorl; 2C. Ventral view of innermost whorl visible and two cross-sections of the next following whorl.

Figures 3A, 3B. *Euryptychites diplotomus* (Koenen, 1902). Upper *Platylenticeras*-Beds, lower lower Valanginian. Sachsenhagen, Northwest Germany. BGR, kv 254, Hannover. The penultimate whorl of a coarsely sculptured and pronouncedly "diplotomous" (i.e. bidichotomous) variant that could also be interpreted as an independent species, x 1. 3A. Lateral view; 3B. Ventral view of the early part of the whorl and its deformed terminal cross-section.


1B
1A
2C
2A
3A
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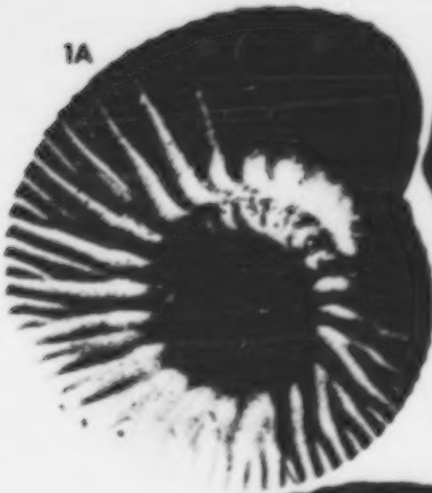
2B

Plate 4

Figures 1A, 1B.	*Propolyptychites quadrifidus* (Koenen, 1902). *Polyptychites*-Beds, lower Valanginian. Bueckeburg-Jetenburg, Northwest Germany. BGR, kv 71, Hannover, x 1. 1A. Lateral view; 1B. Ventral view of the early part of the whorl and its oral cross-section.
Figures 2, 3A, 3B, 4, 5A, 5B	*Polyptychites pavlowi* Koenen, 1902. *Polyptychites*-Beds, Lower Valanginian. Northwest Germany. All photographs x 1.
Figure 2.	Lindhorst, BGR, kv 78, Hannover, Lateral view.
Figures 3A, 3B.	Bueckeburg-Jetenburg, BGR, kv 59, Hannover, 3A. Lateral view; 3B. Ventral view of the oral half of the whorl.
Figure 4.	Bueckeburg-Jetenburg, BGR, kv 65, Hannover. Cross-section of three whorls and the ventral view of the next inner whorl of an entirely septate specimen.
Figures 5A, 5B.	Bueckeburg-Jetenburg, BGR, kv 77, Hannover. 5A. Lateral view; 5B. Ventral view of the oral half of the whorl.
Figures 6A, 6B.	*Polyptychites oerlinghusanus* (Weerth, 1884). Lower *Polyptychites*-Beds, middle part of lower Valanginian. Bueckeburg-Jetenburg, Northwest Germany. BGR, kv 262, Hannover, x 1. 6A. Lateral view; 6B. Ventral view of the oral half of the whorl.
Figure 7.	*Propolyptychites quadrifidus* (Koenen, 1902). Upper *Platylenticeras*-Beds, lower lower Valanginian. Suddendorf, Northwest Germany. Museum "Nature docet", Denekamp, The Netherlands. Juvenile specimen that exhibits the sculpture of different growth stages of the species, x 3.

All specimens figured in this plate, except for those reproduced in Figures 4 and 7, are either adult or nearly adult shells.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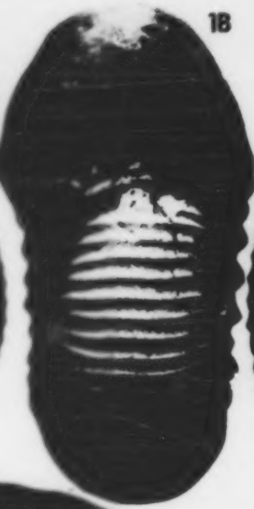
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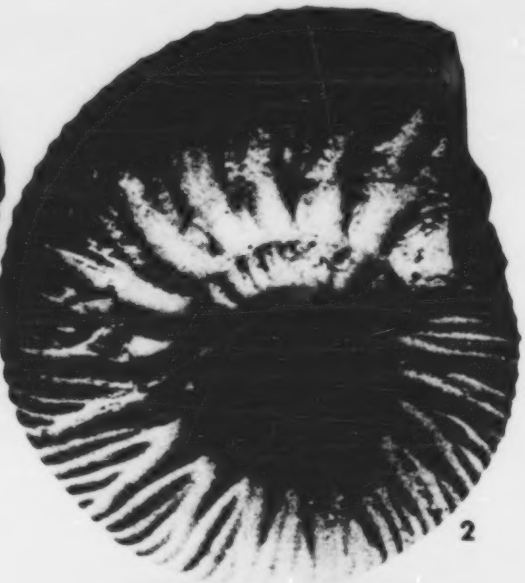
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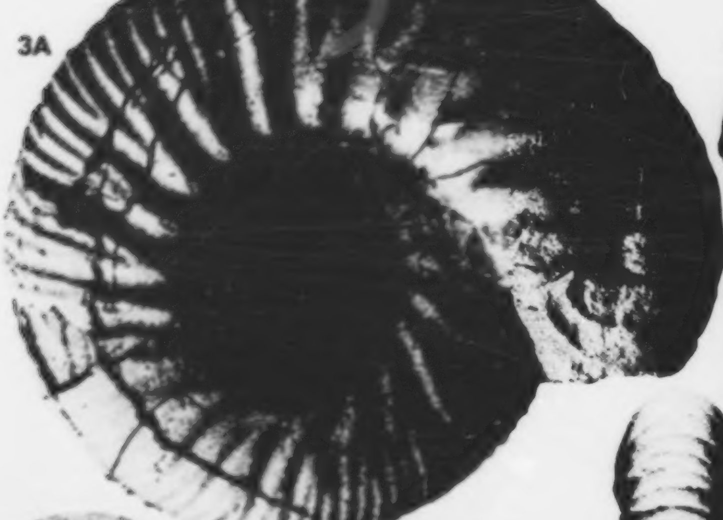
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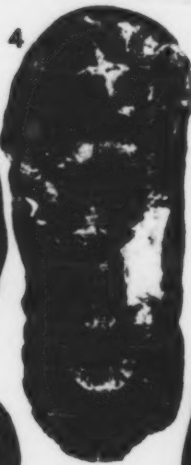
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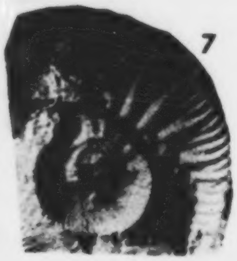
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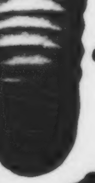
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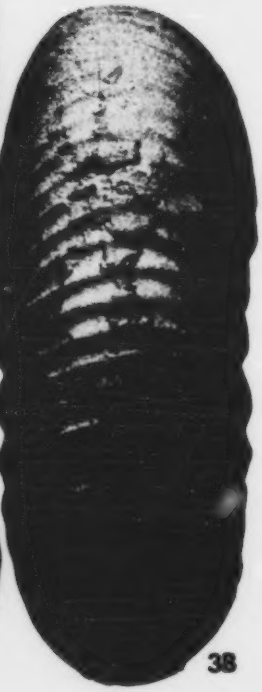
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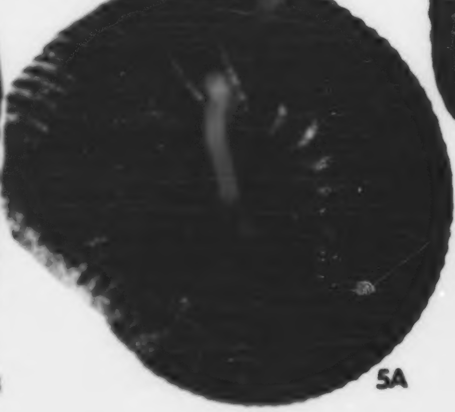
5B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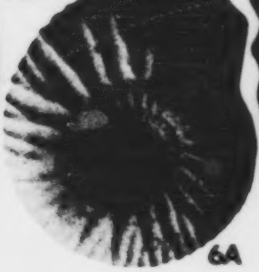
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Plate 5

Figures 1A, 1B.	*Polyptychites pavlowi* Koenen, 1902. *Polyptychites*-Beds, Lower Valanginian. Bueckeburg-Jetenburg, Northwest Germany. BGR, kv 61, Hannover. An adult representative of a coarsely ribbed variant, x 1. 1A. Lateral view; 1B. Ventral view of the oral half of the whorl.
Figure 2.	*Polyptychites pavlowi* Koenen, 1902. Terminal cross-section and ventral view of the early part of the whorl of the specimen reproduced in Pl. 4, fig. 2, see there for further details, x 1.
Figures 3A, 3B, 3C; 5A, 5B.	*Polyptychites ascendens* Koenen, 1902. *Polyptychites*-Beds, lower Valanginian. Bueckeburg-Jetenburg, Northwest Germany. All photographs x 1.
Figures 3A-3C.	BGR, kv 96, Hannover. Intermediate growth stages. 3A. Lateral view; 3B. Terminal cross-section and ventral view of the early part of the whorl; 3C. Lateral view of the other flank.
Figures 5A, 5B.	BGR, kv 94, Hannover. Parts of penultimate and ultimate whorls. 5A. Lateral view; 5B. Ventral view of the oral half of whorl.
Figures 4A, 4B.	*Polyptychites keyserlingi* (Neumayr and Uhlig, 1881). *Polyptychites*-Beds, lower Valanginian. Lindhorst, Northwest Germany. A thick, morphologically progressive variant with a coarse sculpture. An adult or almost adult specimen, which is similar to the lectotype. BGR, kv 81, Hannover. x 1. 4A. Lateral view; 4B. Ventral view of the oral half of the whorl.

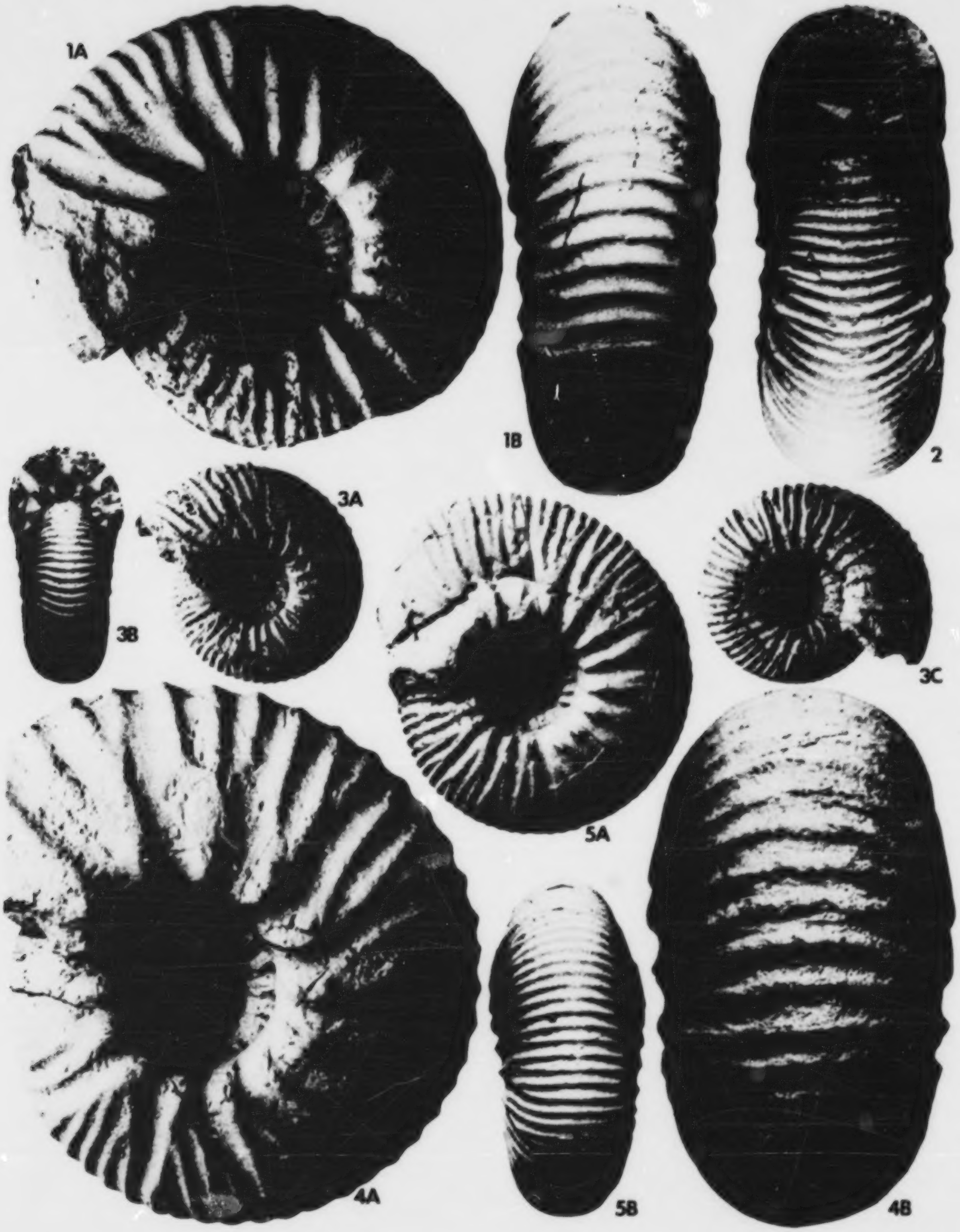
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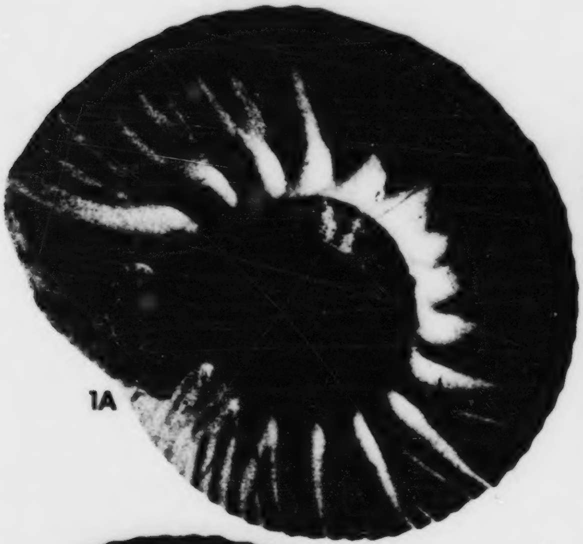
Plate 6

Figures 1A, 1B, 2A, 2B; 3A, 3B; 4A, 4B. *Polyptychites keyserlingi* (Neumayr and Uhlig, 1881). *Polyptychites*-Beds, lower Valanginian. Bueckeburg-Jetenburg, Northwest Germany. Figs. 1 and 3: Variants of the typical form. Figs. 2 and 4: Slender and still morphologically conservative variants. All figured specimens are adult or almost adult shells. All x 1.

Fig. 1. BGR, kv 80, Hannover. 1A. Lateral view; 1B. Ventral view of the early half of the whorl and its terminal cross-section. Fig. 2: BGR, kv 69, Hannover. 2A. Lateral view; 2B. Ventral view of the oral half of the whorl. Fig. 3: BGR, kv 79, Hannover. 3A. Lateral view; 3B. Ventral view of the early half of the whorl and its adoral cross-section. Fig. 4. BGR, kv 75, Hannover. 4A. Lateral view; 4B. Ventral view of the oral half of the whorl.

Figure 5. *Polyptychites oerlinghusansus* (Weerth, 1884). *Polyptychites*-Beds, lower Valanginian. Bueckeburg-Jetenburg, Northwest Germany. BGR, kv 264, Hannover. Lateral view of an adult representative, x 1. Other views of this specimen on Pl. 7, figs. 3A-3C.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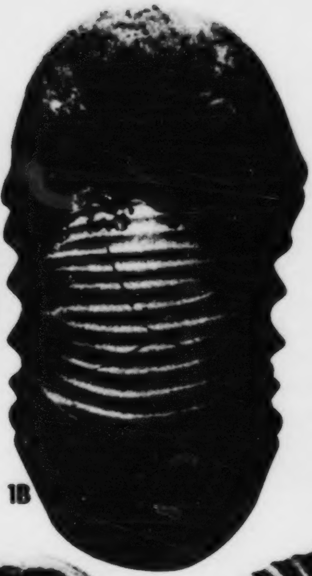
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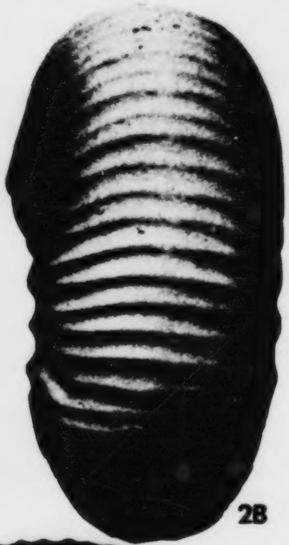
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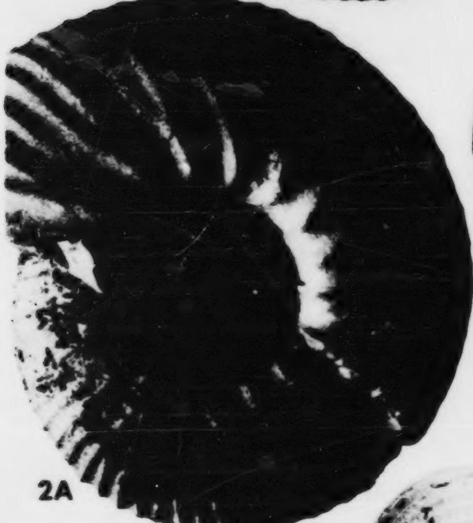
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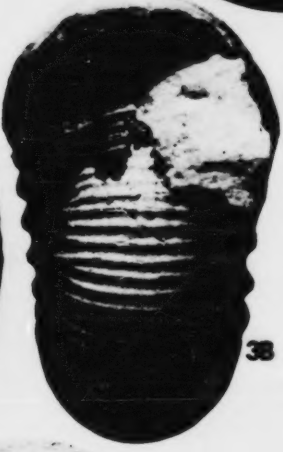
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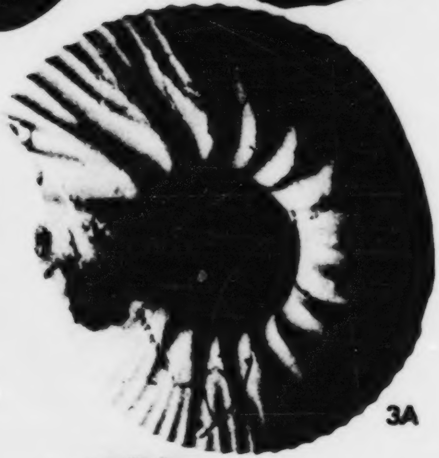
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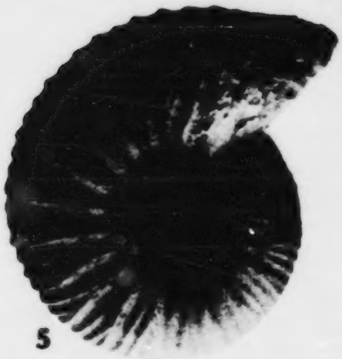
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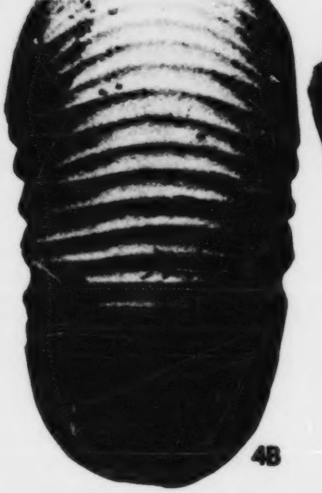
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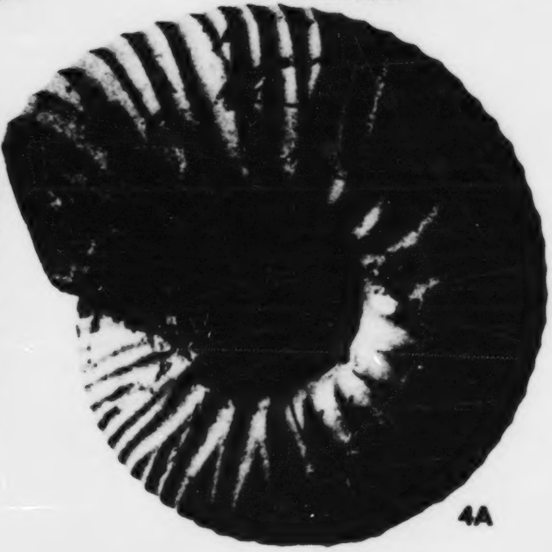
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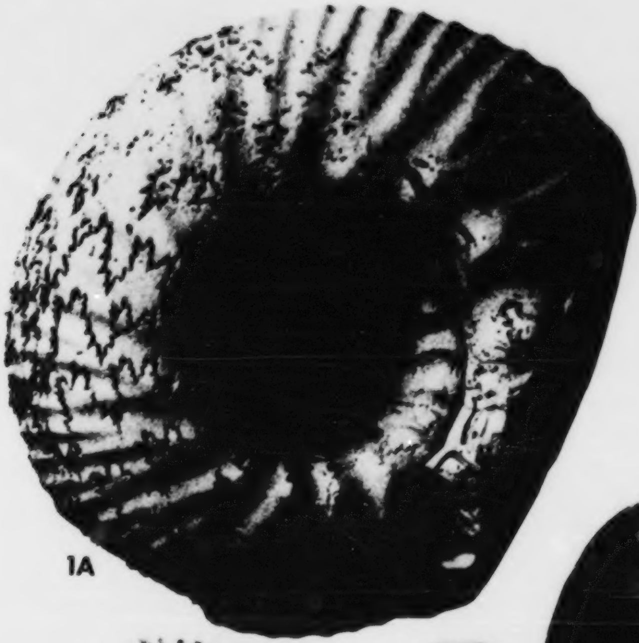
Plate 7

Figures 1A, 1B.	*Polyptychites lamplughi* Pavlow, 1892. *Polyptychites*-Beds, lower Valanginian. Bueckeburg-Jetenburg, Northwest Germany. BGR, kv 84, Hannover. Penultimate whorl with the beginning of the living chamber, x 1. 1A. Lateral view of undeformed side; 1B. Ventral view of partly deformed oral half of the whorl.
Figures 2A, 2B.	*Polyptychites ascendens* Koenen, 1902. *Polyptychites*-Beds, lower Valanginian. Bueckeburg-Jetenburg, Northwest Germany. BGR, kv 95, Hannover. A typical representative with the beginning of adult living chamber, x 1. 2A. Lateral view; 2B. Ventral view of the oral half of the whorl.
Figures 3A-3C.	*Polyptychites oerlinghusanus* (Weerth, 1884). *Polyptychites*-Beds, lower Valanginian. Bueckeburg-Jetenburg, BGR kv 264, Hannover. An adult specimen that is also reproduced in Pl. 6, fig. 5, x 1. 3A. Lateral view; 3B. Ventral view of the early half of the whorl and its terminal cross-section; 3C. Ventral view of the oral half of the whorl.
Figures 4, 5.	*Polyptychites* aff. *keyserlingi* (Neumayr and Uhlig, 1881). *Polyptychites*-Beds, lower Valanginian. This form group differs from *P. keyserlingi* s. str. in finer ribs and an almost fasciculate character of rib bundles. Its separation as an independent species may become advisable when more material becomes available. Figure 4. A lateral view only, BGR, kv 274, Hannover. A well preserved penultimate whorl with the beginning of the adult living chamber, x 1. Fig. 5. A ventral view only, BGR, kv 273, Hannover. x 1.
Figure 6.	*Paratollia kemperi* Casey, 1973. Holotype. Upper *Platylenticeras*-Beds, lower lower Valanginian. Suddendorf, Northwest Germany. BGR, kv 341, Hannover. Lateral view. The last half whorl is an adult(?) living chamber, x 1.
Figures 7, 8.	*Bodylevskites pumilio* (Vogel, 1959). Lower *Polyptychites*-Beds, middle part of lower Valanginian. Bueckeburg-Jetenburg, Northwest Germany. All figures x 2. Fig. 7A, 7B. BGR, kv 253, Hannover. 7A. Lateral view; 7B. Ventral view. Fig. 8A, 8B. BGR, kv 354, Hannover. 8A. Lateral view; 8B. Ventral view.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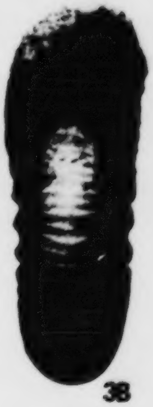
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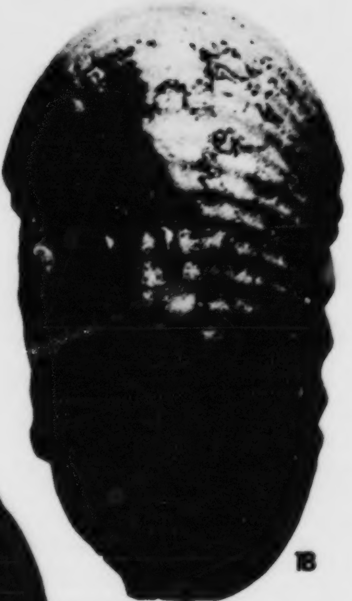
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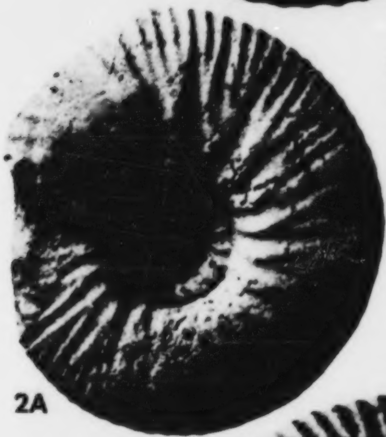
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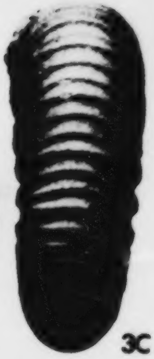
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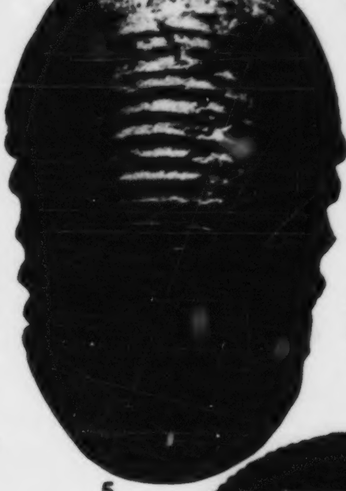
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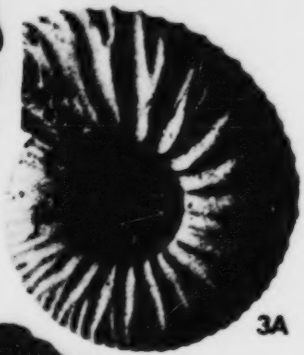
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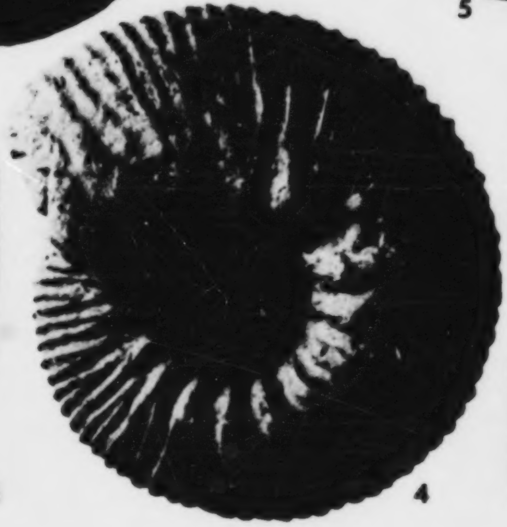
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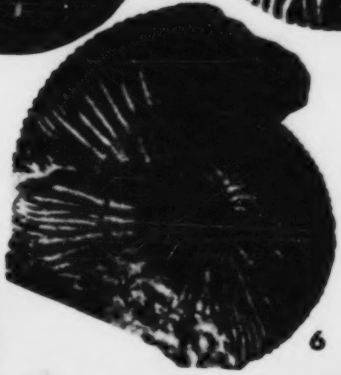
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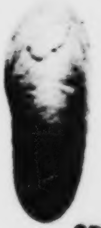
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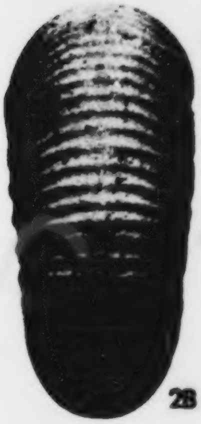
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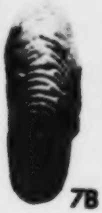
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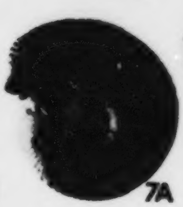
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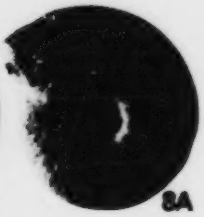

8A

Plate 8

Figures 1A-1C.	*Polyptychites ramulicosta* Pavlow, 1892. *Polyptychites*-Beds, lower Valanginian. Lindhorst, Northwest Germany. BGR, kv 301, Hannover. A morphologically progressive variant. 1A and 1B. Lateral and ventral views of an apparently penultimate whorl. 1C. Fragment of an adult living chamber(?) of the same specimen. All figures x 1.
Figures 2; 3A, 3B; 4A, 4B.	*Polyptychites multicostatus* Koenen, 1909. *Polyptychites*-Beds, Lower Valanginian. Northwest Germany. All figures x 1. Fig. 2. Lindhorst, BGR, kv 103, Hannover. An adult or almost adult specimen. Fig. 3. Lindhorst, BGR, kv 104, Hannover. A thick variant represented predominantly by a penultimate whorl. 3A. Lateral view; 3B. Ventral view of the oral half of the whorl. Fig. 4. Bueckeburg-Jetenburg, BGR, kv 107, Hannover. An adult or almost adult representative of a slender variant. 4A. Lateral view of two successive whorls; 4B. Cross-section of the last preserved whorl and ventral view of the preceding whorl. The ventral view of the last preserved whorl is shown in Pl. 9, fig. 2.
Figures 5A-5C.	*Bodylevskites pumilio* (Vogel, 1959). Lower *Polyptychites*-Beds, middle part of lower Valanginian. Bueckeburg-Jetenburg, Northwest Germany. BGR, kv 355, Hannover. Note a well developed constriction. 5A. Lateral view, x 1; 5B. Same lateral view, as last, x 1.5; 5C. Ventral view of the oral half of the whorl, x 2.

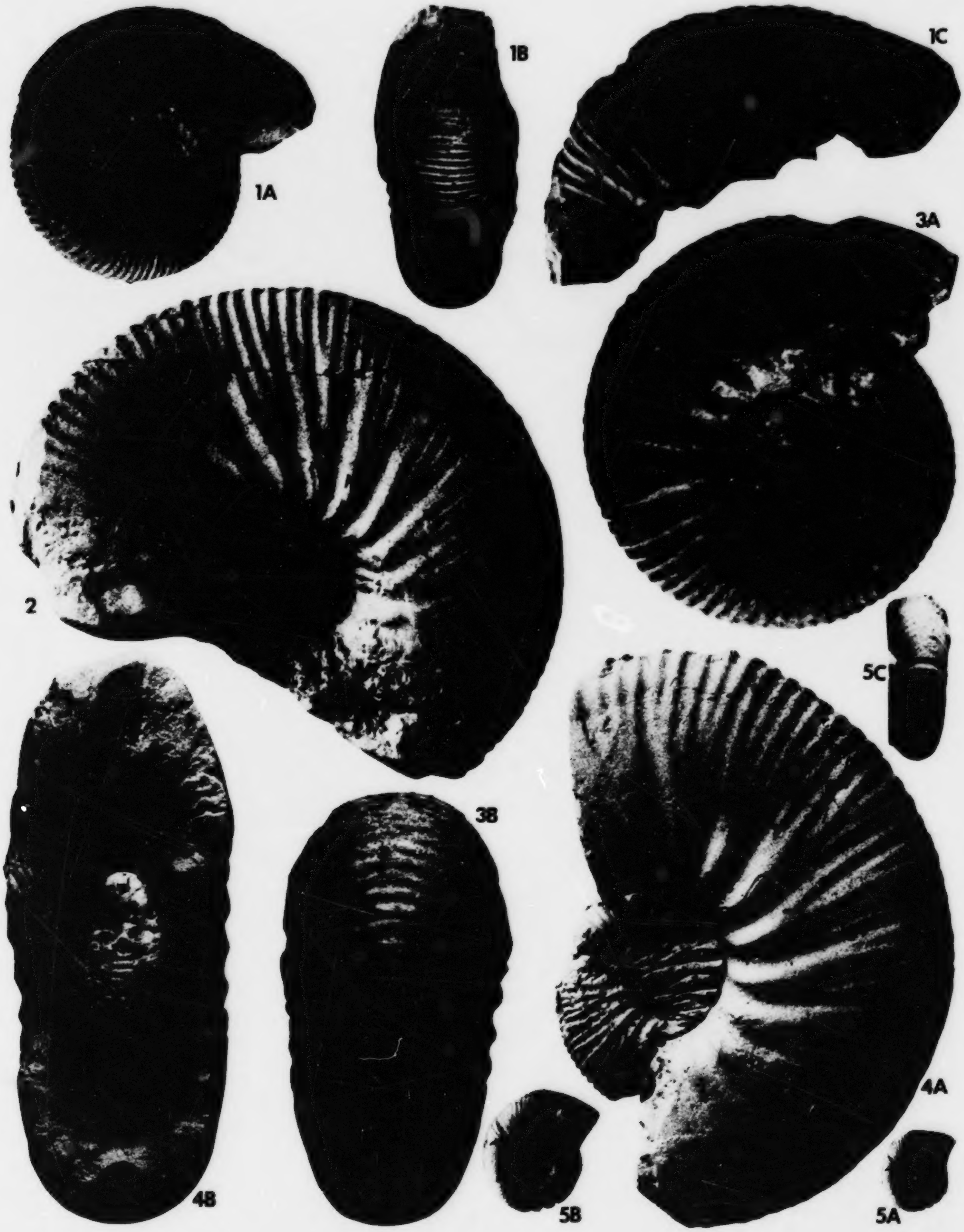
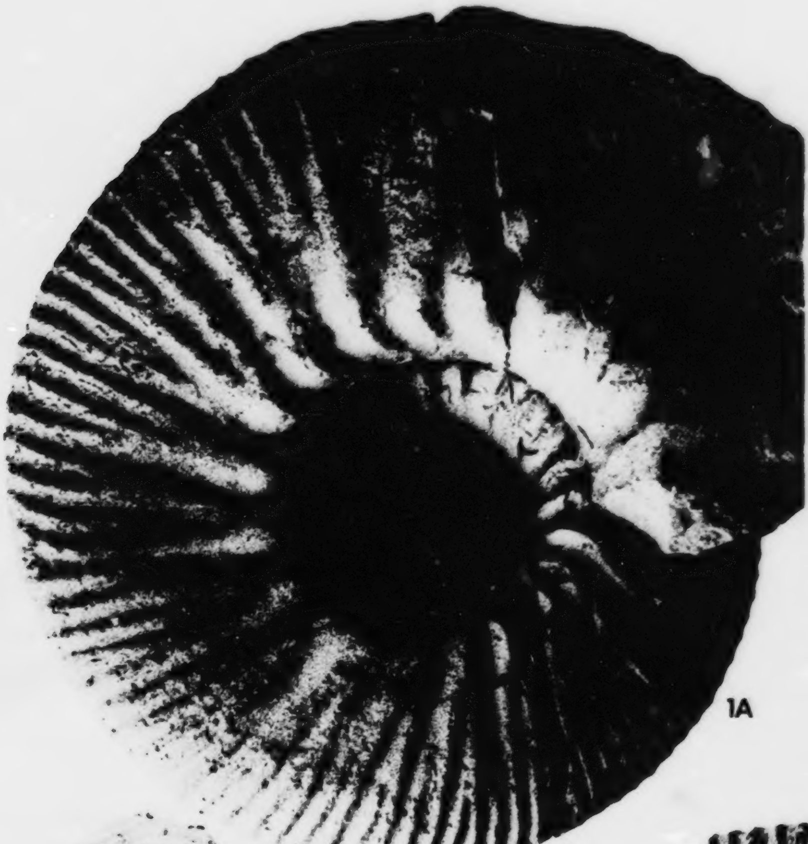

1A
1B
1C
3A
2
5C
3B
4A
4B
5B
5A

Plate 9

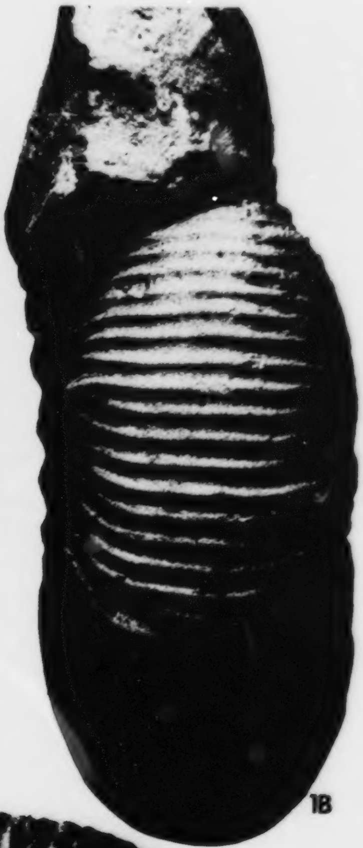
Figures 1A, 1B, 2. *Polyptychites multicostatus* Koenen, 1909. *Polyptychites*-Beds, lower Valanginian. Lindhorst, Northwest Germany. All figures, x 1. Fig. 1. BGR, kv 98, Hannover. A presumably adult specimen. 1A. Lateral view; 1B. Ventral view of the early half of the whorl. Fig. 2. BGR, kv 107, Hannover. Ventral view of the specimen shown in Pl. 8, figs. 4A, 4B.

Figures 3A, 3B. *Polyptychites hapkei* n. sp. Zone of *Prodichotomites hollwedensis*, basal upper Valanginian. Twiehausen, Northwest Germany. BGR, kv 91, Hannover. Fragment of an intermediate whorl. This specimen has a typical ribbing habit characterized by the prevalence of bidichotomous bundles, x 1. 3A. Lateral view; 3B. Ventral view.

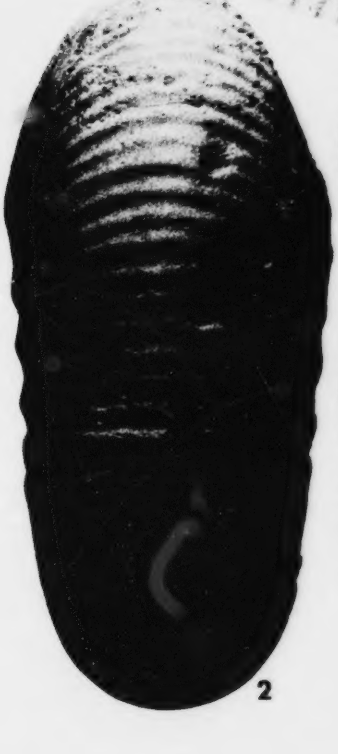
Figures 4A-4C. *Polyptychites hapkei* n. sp. The same age and locality as for the specimen reproduced in Fig. 3. BGR, kv 284, Hannover. This specimen already exhibits the change of the whorl shape and proportions that is so typical for the species. This is illustrated by Fig. 4C that reproduces the fragment of the whorl that follows immediately that whorl reproduced in Figs. 4A and 4B. The ventral view of this fragment is reproduced in Pl. 13, fig. 2. The originally narrow whorl section suddenly increases strongly in width. This results in the appearance of almost *Euryptychites*-like proportions of the cross-section in the intermediate growth stages. All figures x 1. 4A. Lateral view of an early whorl; 4B. Ventral view of the oral half of that whorl; 4C. Cross-section of the next following whorl.



1A



1B



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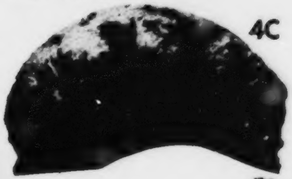
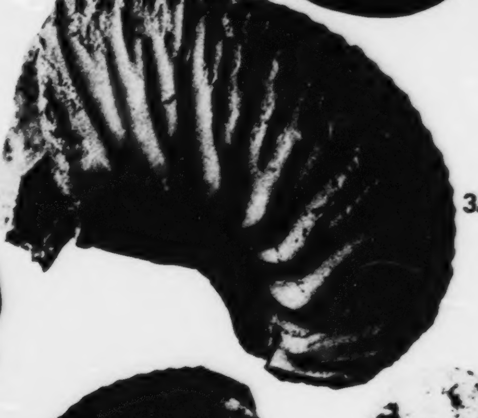
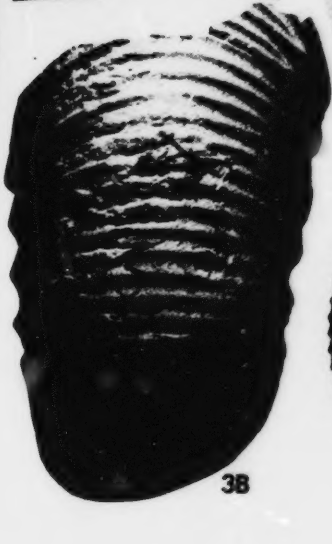


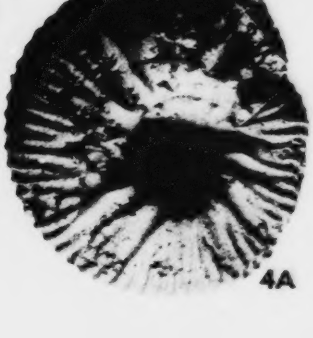
4C



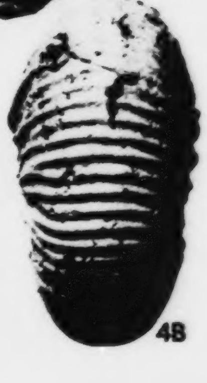
3A



3B



4A



4B

Plate 10

Figures 1A, 1B. *Polyptychites orbitatus* Koenen, 1902. Zone of *Prodichotomites hollwedensis*, basal upper Valanginian. Twiehausen, Northwest Germany, BGR, kv 280, Hannover. Note the slender juvenile whorls with their fine and closely spaced sculpture, x 1. 1A. Cross-section of outer whorls and ventral view of an intermediate whorl; 1B. Lateral view of the same whorls.

Figures 2A-2C. Transitional form between *Polyptychites pavlowi* Koenen, 1902 and *P. ascendens* Koenen, 1902. *Polyptychites*-Beds, lower Valanginian, Bueckeburg-Jetenburg, Northwest Germany. BGR, kv 265, Hannover. Presumably the penultimate whorl, x 1. 2A. Lateral view; 2B. Ventral view of the early half of the whorl and its terminal cross-section; 2C. Ventral view of the oral half of the whorl.

Figure 3. *Polyptychites hapkei* n. sp. Holotype. Zone of *Prodichotomites hollwedensis*, basal upper Valanginian. Hollwede II, Northwest Germany. BGR, kv 285, Hannover. An adult living chamber characterized by a sculpture with senile features, x 1. See Pl. 28, fig. 2 for the ventral view.

Figures 4A-4C. *Bodylevskites pumilio* (Vogel, 1959). Lower *Polyptychites*-Beds, middle part of lower Valanginian. Bueckeburg-Jetenburg, BGR, kv 359, Hannover. 4A. Lateral view, x 1; 4B. Lateral view of the other side, x 1.5; 4C. Whorl's cross-section, x 2.

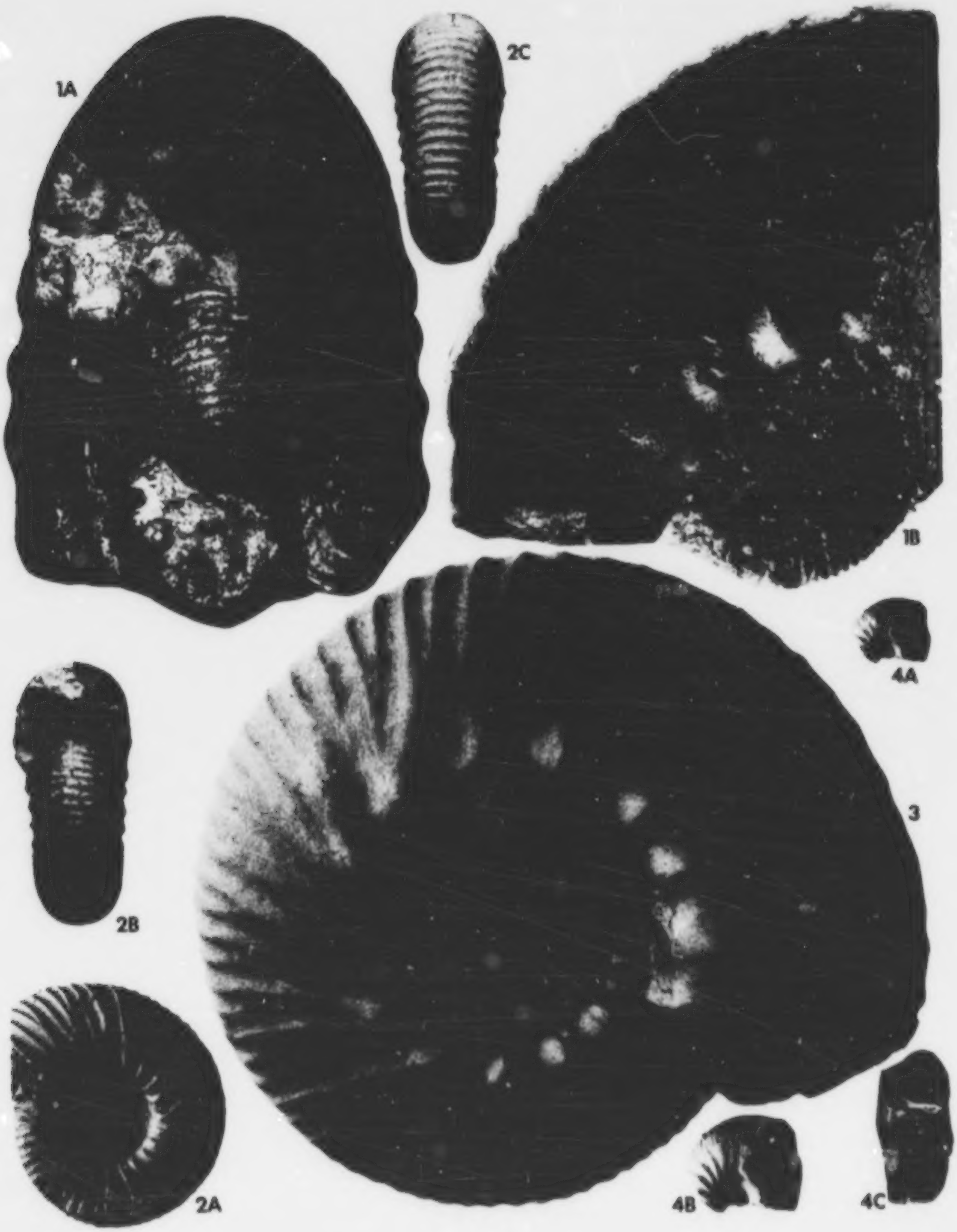

1A
2C
1B
4A
3
2B
2A
4B
4C

Plate 11

Figures 1A, 1B. *Polyptychites hapkei* n. sp. Zone of *Prodichotomites hollwedensis*, basal upper Valanginian. Hollwede II, Northwest Germany, BGR, kv 92, Hannover. A presumably penultimate whorl with a very typical bundling habit, x 1. 1A. Lateral view; 1B. Ventral view.

Figures 2A, 2B. *Polyptychites ramulicosta* Pavlow, 1892. *Polyptychites*-Beds, lower Valanginian. Lindhorst, Northwest Germany. BGR, kv 319, Hannover. A rather conservative variant; compare it with the specimen reproduced in Pl. 8, fig. 1. The casts of juvenile whorls of this specimen are reproduced in Pl. 12, figs. 3A-3C. 2A. Lateral view; 2B. Ventral view, x 1.

Figure 3. *Polyptychites saxonicus* n. sp. Zone of *Prodichotomites hollwedensis*, basal upper Valanginian. Hollwede II, Northwest Germany. BGR, kv 114, Hannover. A presumably adult living chamber that exhibits a distinct weakening of the sculpture. Lateral view, x 1. See Pl. 12, fig. 4 for the ventral view.

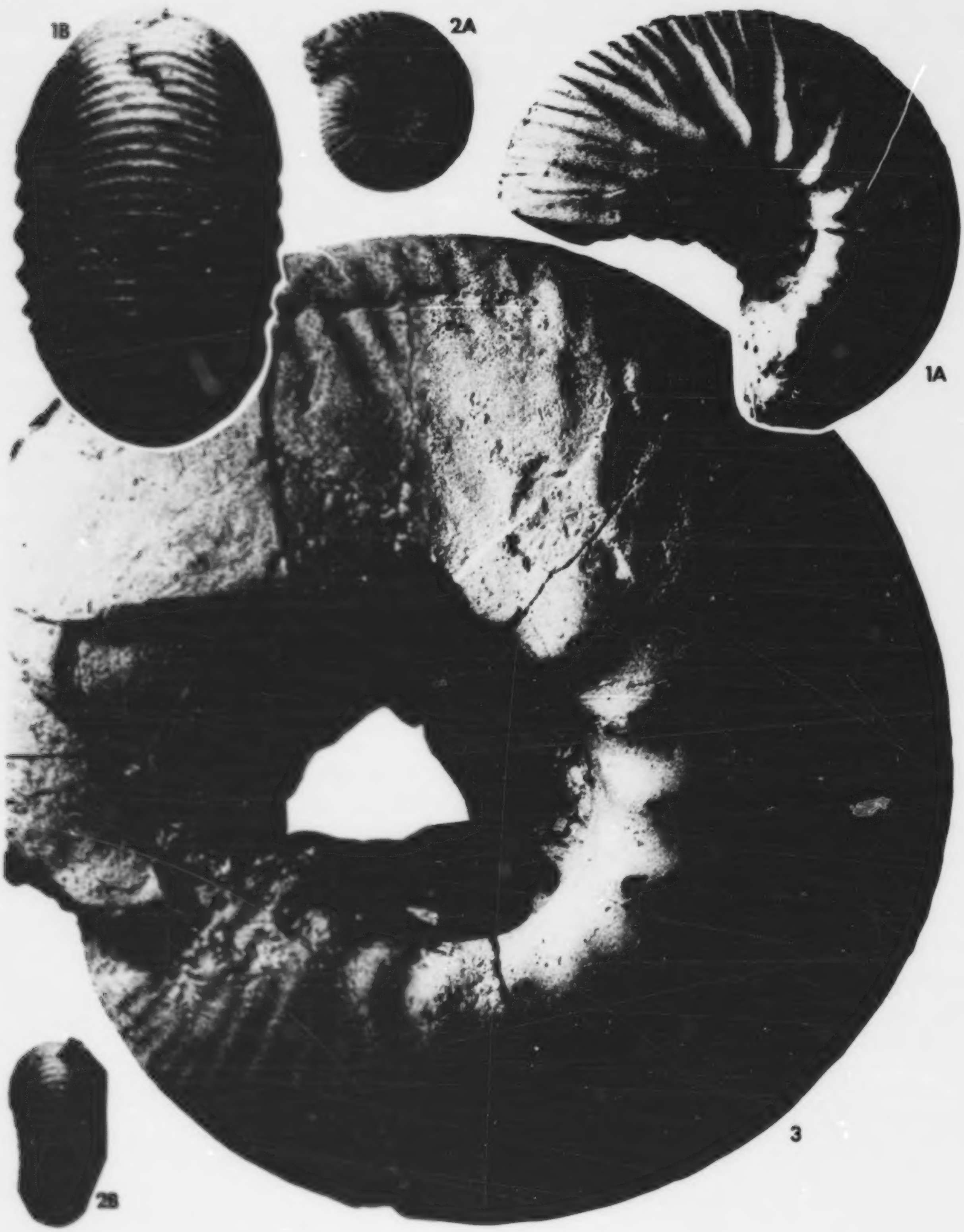

1B
2A
1A
3
2B

Plate 12

Figure 1.	*Polyptychites* aff. *saxonicus* n. sp. Basal upper Valanginian, Hoheneggelsen, Brandes-Collection, Northwest Germany. GIH Type No. 2516. Photograph of plaster cast preserved in BGR, kv 110, Hannover. The specimen is presumed to be largely a penultimate whorl. Lateral view, x 1. Ventral view is reproduced in Pl. 13, fig. 3.
Figures 2A, 2B.	*Polyptychites saxonicus* n. sp. Holotype. Basal upper Valanginian(?). Hoheneggelsen, Northwest Germany. Brandes-Collection, GIH Type No. 2517. Photograph of plaster cast preserved in BGR, kv 109, Hannover. A fragment of an entirely septate specimen, the oralmost part of which presumably represents the penultimate whorl, x 1. 2A. Lateral view; 2B. Oralmost cross-section and the ventral view of preceding whorl.
Figures 3A-3C.	*Polyptychites ramulicosta* Pavlow, 1892. Plaster casts of juvenile whorls of the specimen reproduced in Pl. 11, fig. 2. See there for further details. All photographs x 1. 3A. Lateral view; 3B. Lateral view of the next younger whorl; 3C. Ventral view and terminal cross-section of the whorl shown in 3A.
Figure 4.	*Polyptychites saxonicus* n. sp. Ventral view of the specimen reproduced in Pl. 11, fig. 3. See there for further details, x 1.

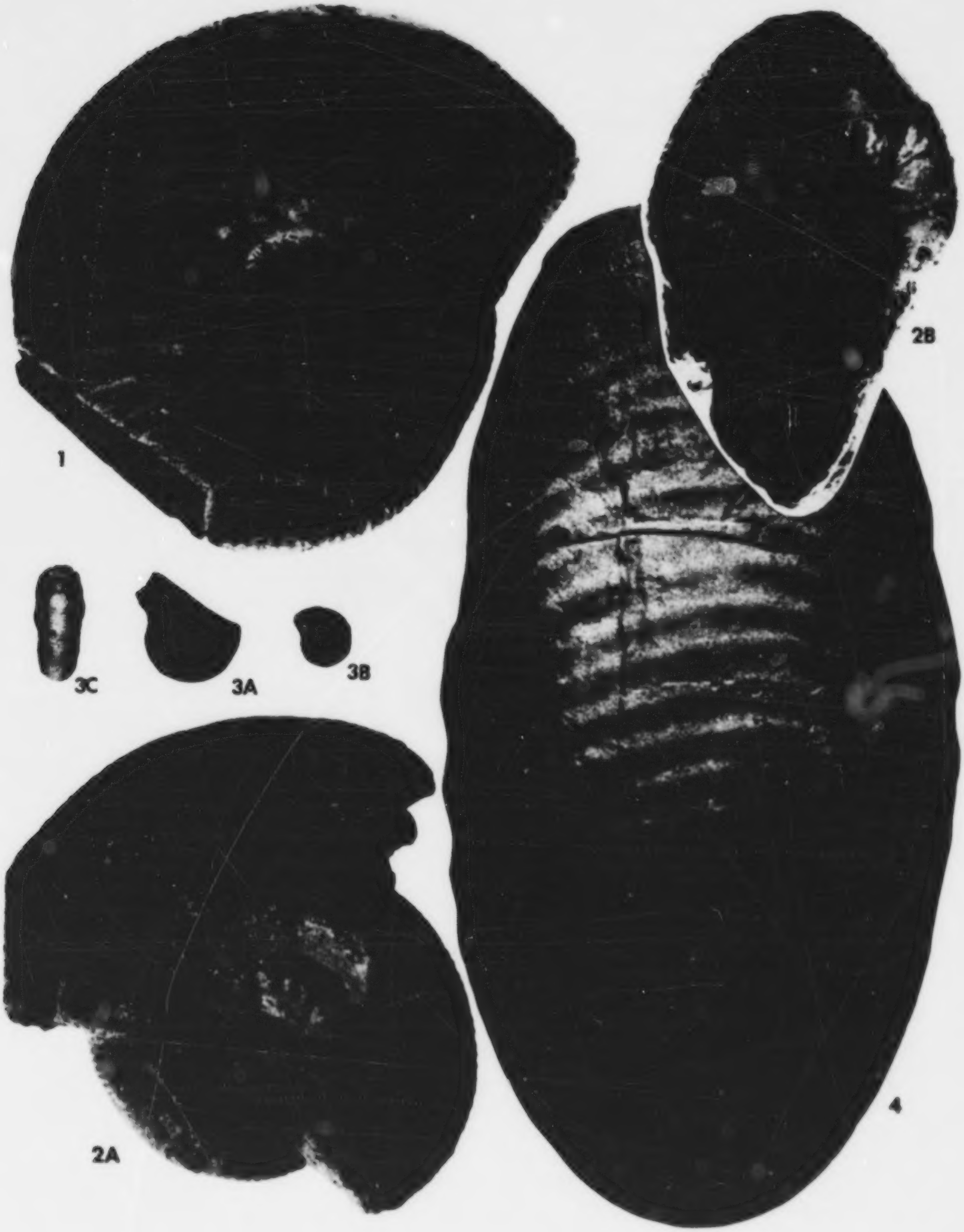
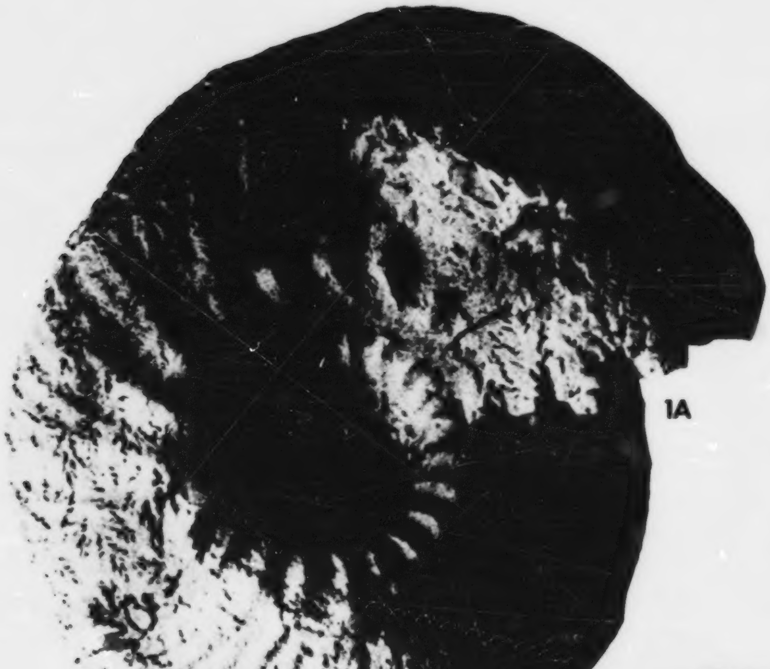

1
2B
3C
3A
3B
2A
4

Plate 13

Figures 1A, 1B.	*Polyptychites tethyale* n. sp. Zone of *Prodichotomites hollwedensis*, basal upper Valanginian. Twiehausen, Northwest Germany. BGR, kv 282, Hannover. A slightly deformed specimen that is septate throughout, x 1. 1A. Lateral view; 1B. Terminal cross-section and ventral view of the early half of the whorl.
Figure 2	*Polyptychites hapkei* n. sp. Ventral view of the specimen reproduced in Pl. 9, fig. 4C. See there for further details, x 1.
Figure 3	*Polyptychites* aff. *saxonicus* n. sp. Ventral view of the specimen reproduced in Pl. 12, fig. 1. See there for further details, x 1.
Figures 4A, 4B.	*Polyptychites orbitatus* Koenen, 1902. Plaster cast of the destroyed holotype. Basal upper Valanginian(?). Hoheneggelsen, Northwest Germany. Plaster casts in GIG and BGR, kv 278, Hannover, x 1. 4A. Lateral view; 4B. Terminal cross-section and ventral view of the early half of the whorl.



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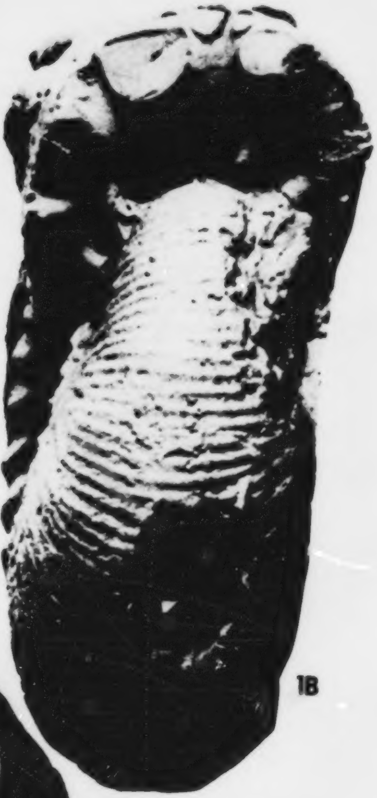
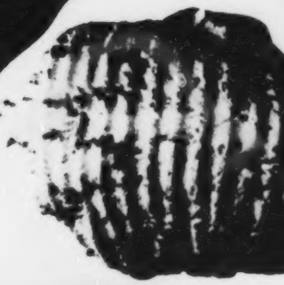


1B



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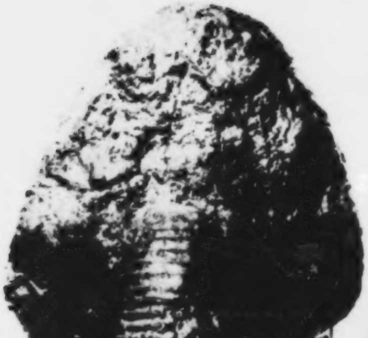

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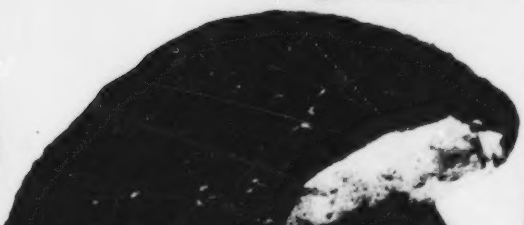

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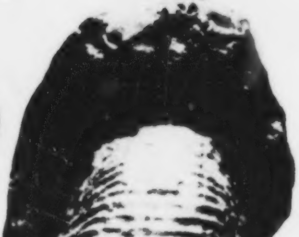


4B

Plate 14

Figures 1A, 1B; 2A, 2B. *Prodichotomites robustus* n. sp. Lower upper Valanginian. Hollwede II, Northwest Germany. All photographs x 1. Fig. 1. BGR kv 292, Hannover. 1A. Lateral view; 1B. Ventral view.

Fig. 2: Holotype, BGR, kv 291, Hannover. The same locality and age as for the specimen shown in fig. 1. 2A. Lateral view; 2B. Ventral view.

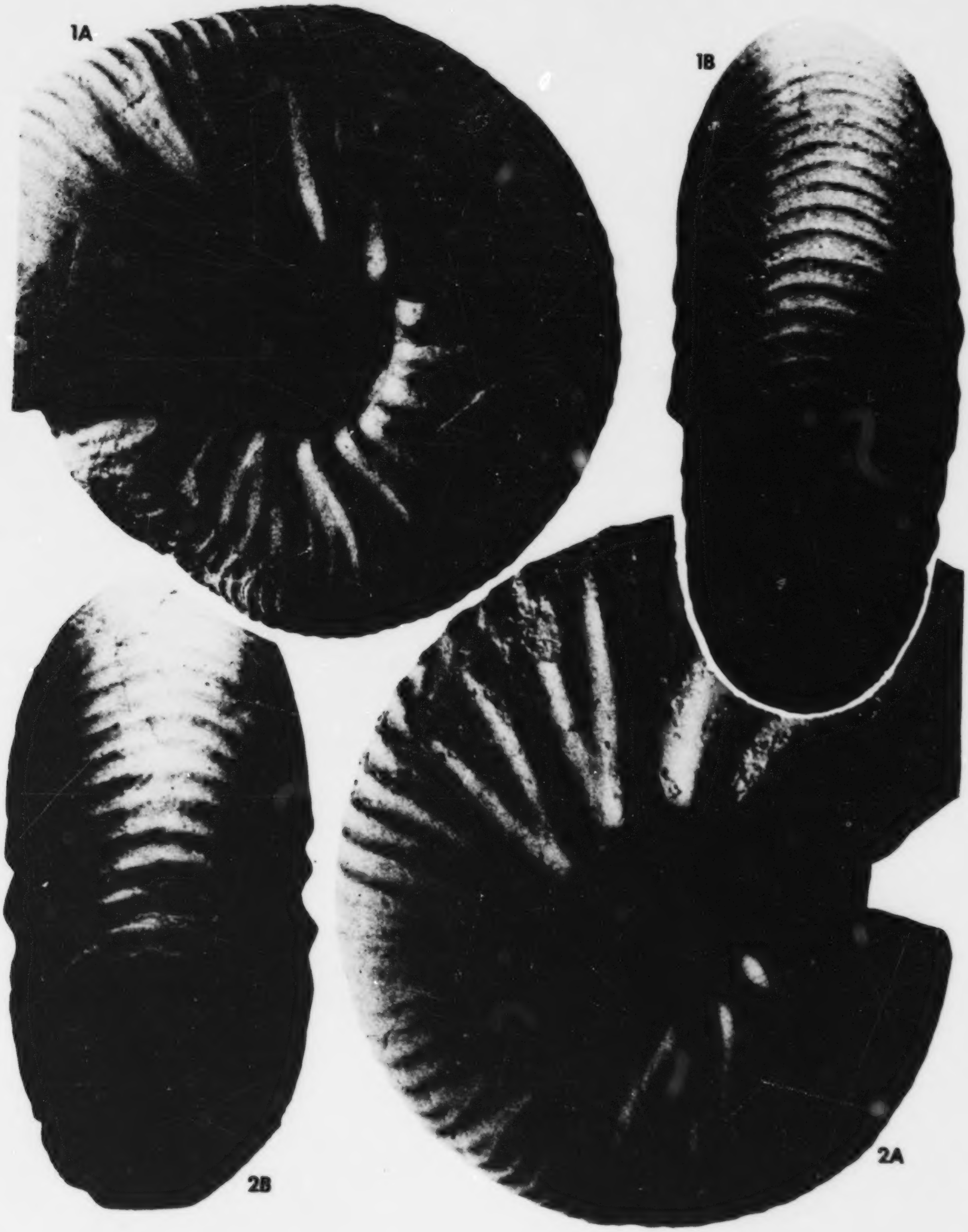
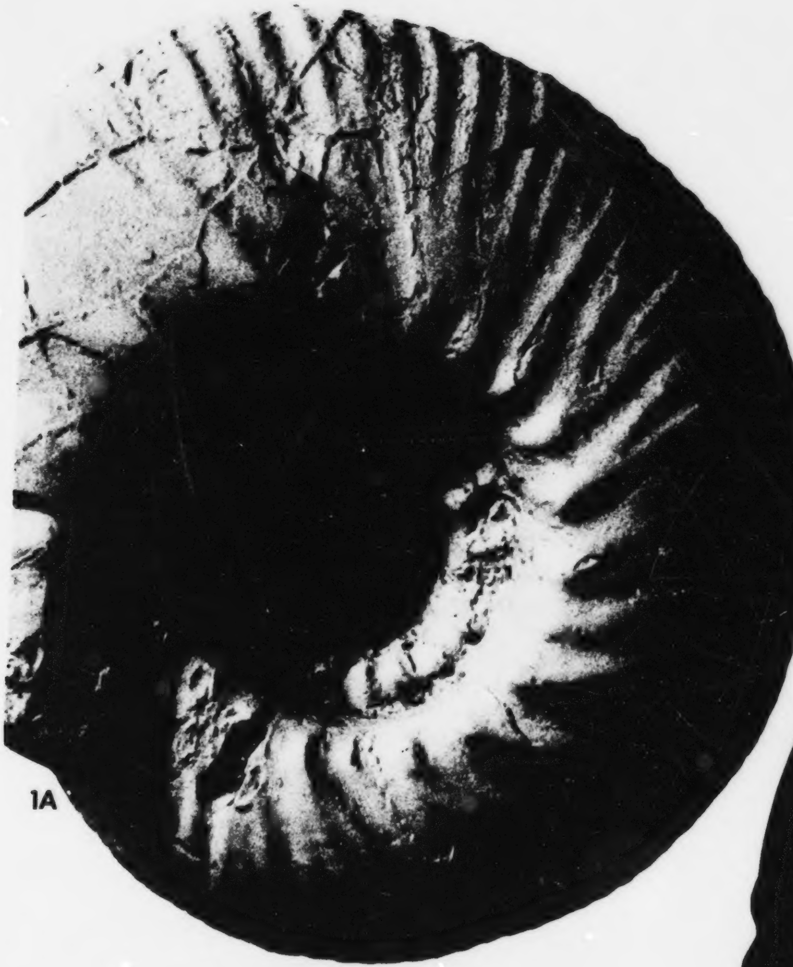

1A
1B
2B
2A

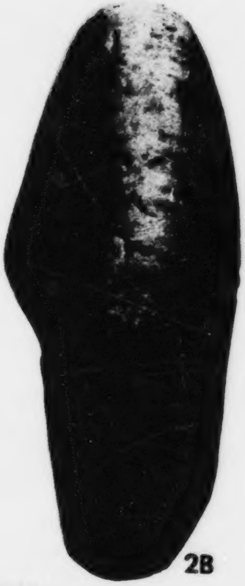
Plate 15

Figures 1A, 1B. *Prodichotomites pfaffi* n. sp. Holotype. Zone of *Prodichotomites hollwedensis*, basal upper Valanginian. Twiehausen, Northwest Germany. BGR, kv 290, Hannover. A presumably adult shell, x 1. 1A. Lateral view; 1B. Ventral view.

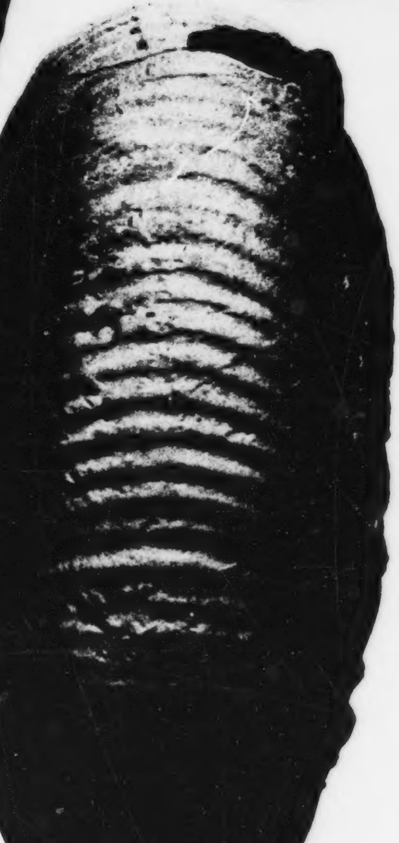
Figures 2A, 2B. *Prodichotomites complanatus* (Koenen, 1902). Zone of *Prodichotomites hollwedensis*, basal upper Valanginian. Twiehausen, Northwest Germany. BGR, kv 298, Hannover. A completely septate shell. It appears to represent the penultimate whorl, for the most part at least, x 1. 2A. Lateral view; 2B. Ventral view of the oral half of the whorl.



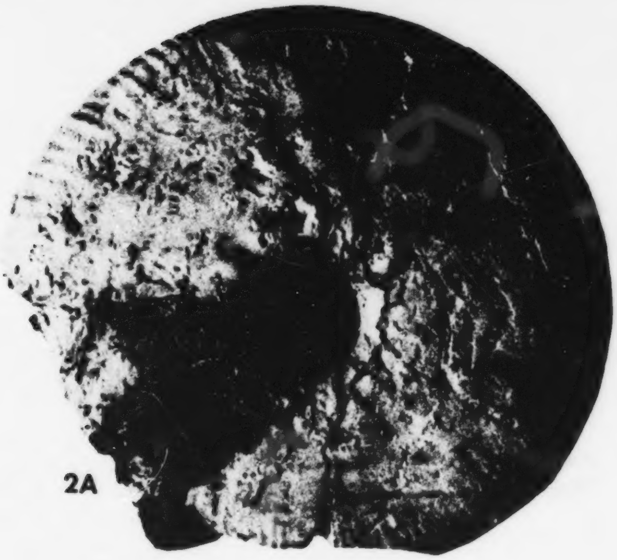
1A



2B



1B

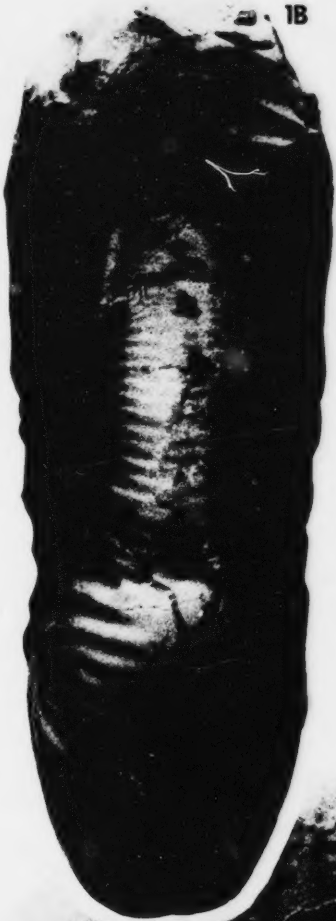


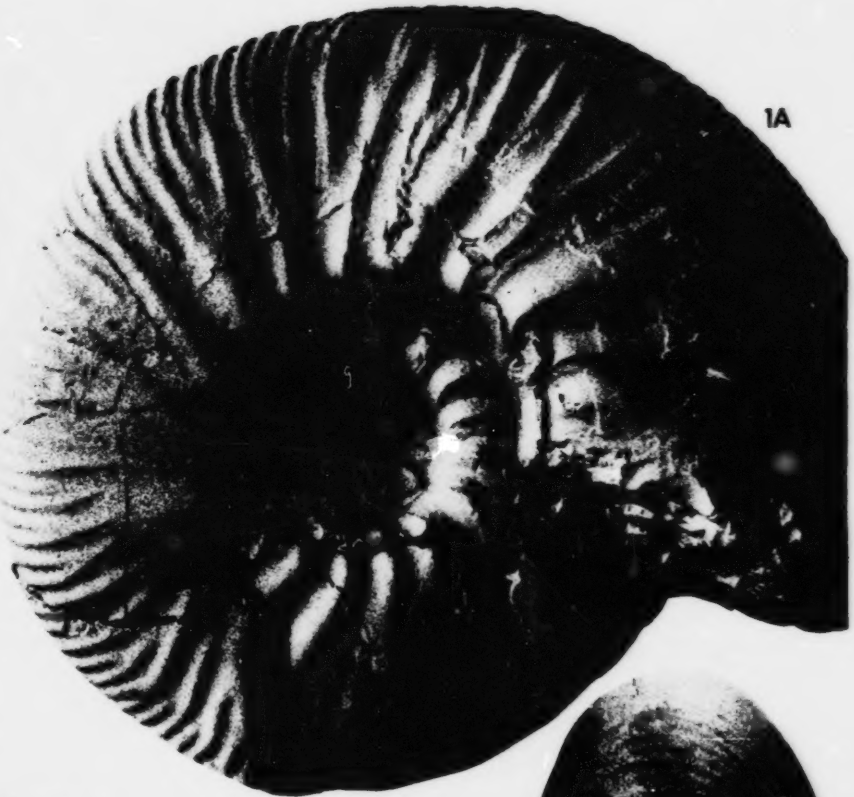
2A

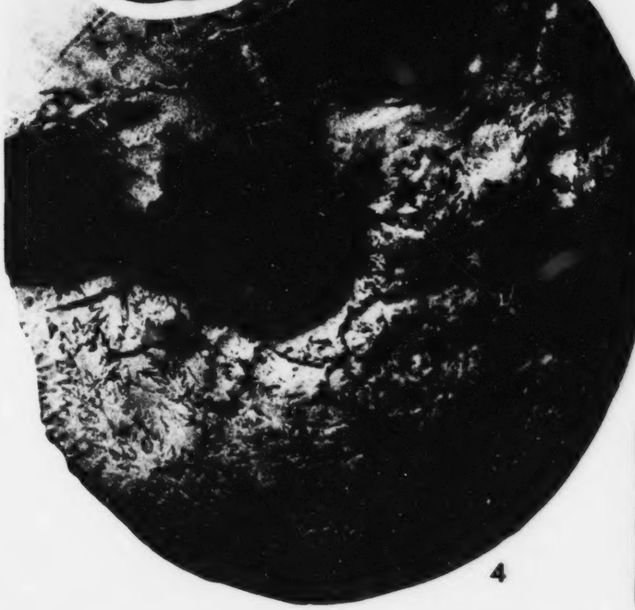
Plate 16

Figures 1A-1C.	A transitional form connecting *Prodichotomites hollwedensis* Kemper, 1978 with *P. polytomus* (Koenen, 1902). Zone of *Prodichotomites hollwedensis*, basal upper Valanginian. Twiehausen, Northwest Germany. BGR, kv 119, Hannover. An adult shell, x 1. 1A. Lateral view. Note a strong pathological disorganization of the sculpture on the early third of the whorl; 1B. Terminal cross-section and the ventral view of the early half of the whorl. Note the injury and the resulting strong disorganization of ornament; 1C. Ventral view of the oral half of the whorl.
Figure 2.	*Prodichotomites flexicosta* (Koenen, 1902). BGR, kv 295, Hannover. See Pl. 22, fig. 2 for the lateral view. Ventral view, x 1.
Figure 3.	*Prodichotomites* juven. ex gr. *P. hollwedensis* Kemper 1978 — *P. flexicosta* (Koenen, 1902). BGR, kv 297, Hannover, x 1.
Figure 4	*Prodichotomites complanatus* (Koenen, 1902). BGR, kv 124, Hannover. Lateral view of a morphologically progressive variant. The last quarter-whorl is obviously an adult living chamber, x 1.

The specimens in Figs 2-4 are from Twiehausen, Northwest Germany.


1B


1A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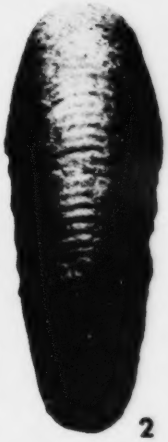
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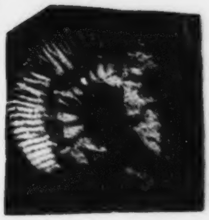
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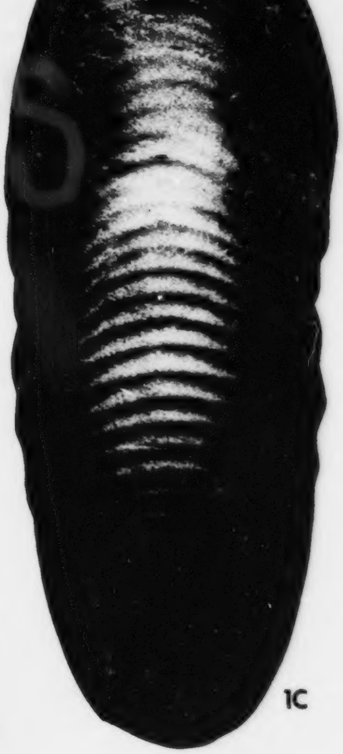

1C

Plate 17

Figures 1A, 1B. *Prodichotomites flexicosta* (Koenen, 1902). Basal upper Valanginian. Hollwede, Northwest Germany. BGR, kv 123, Hannover. Though the specimen is postmortally laterally compressed, it appears nevertheless to represent a slender variant, which possesses a prominent sculpture on the upper part of flanks. The specimen represents mostly the penultimate whorl, x 1. 1A. Lateral view; 1B. Terminal cross-section and ventral view of the early half of the whorl.

Figures 2A, 2B. *Prodichotomites flexicosta* (Koenen, 1902). Age and locality as for the specimen reproduced in Fig. 1. Original in the collection of GIH. Plaster cast in BGR, kv 296, Hannover. A typical specimen with the preserved earliest part of adult living chamber, x 1. 2A. Lateral view; 2B. Ventral view.

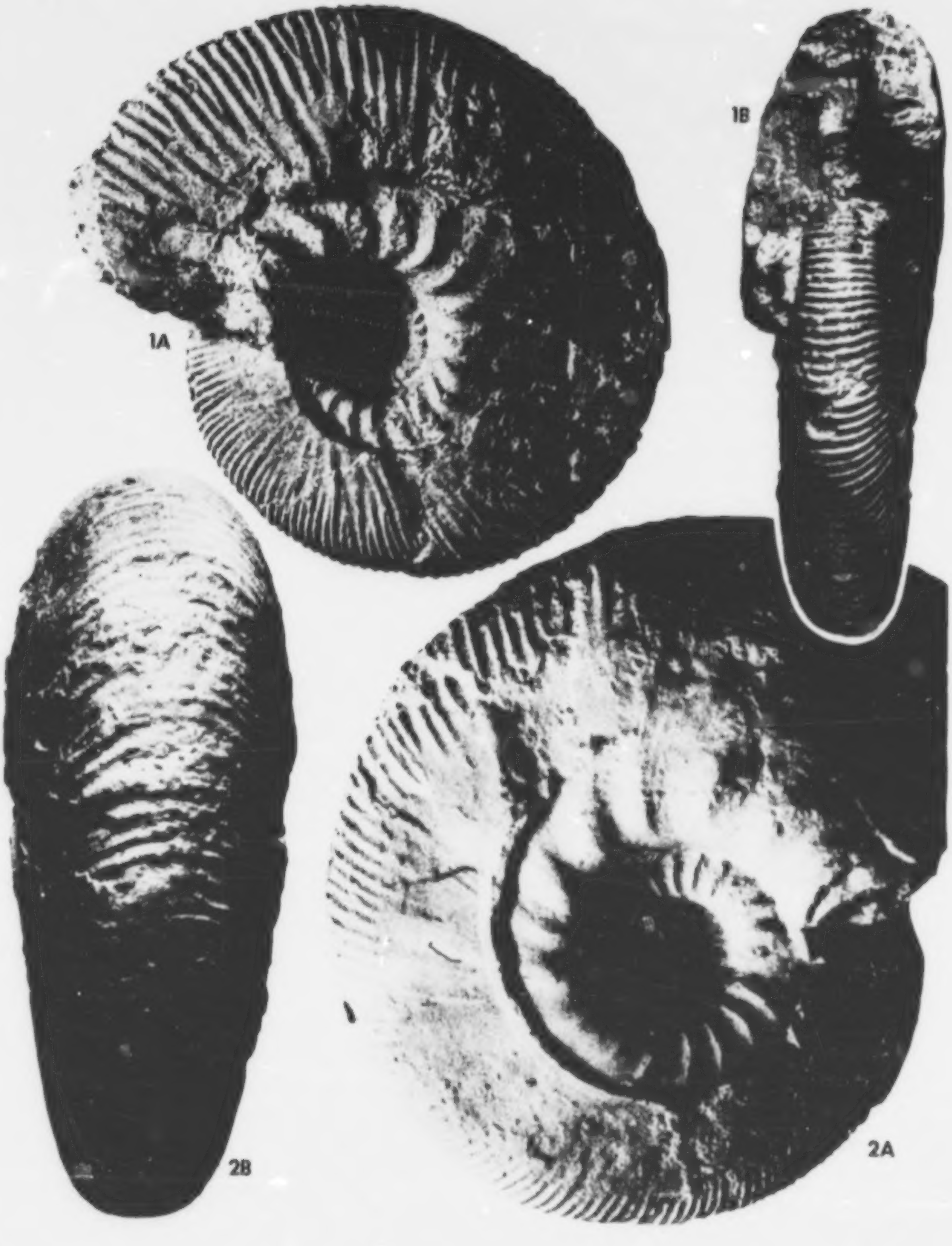
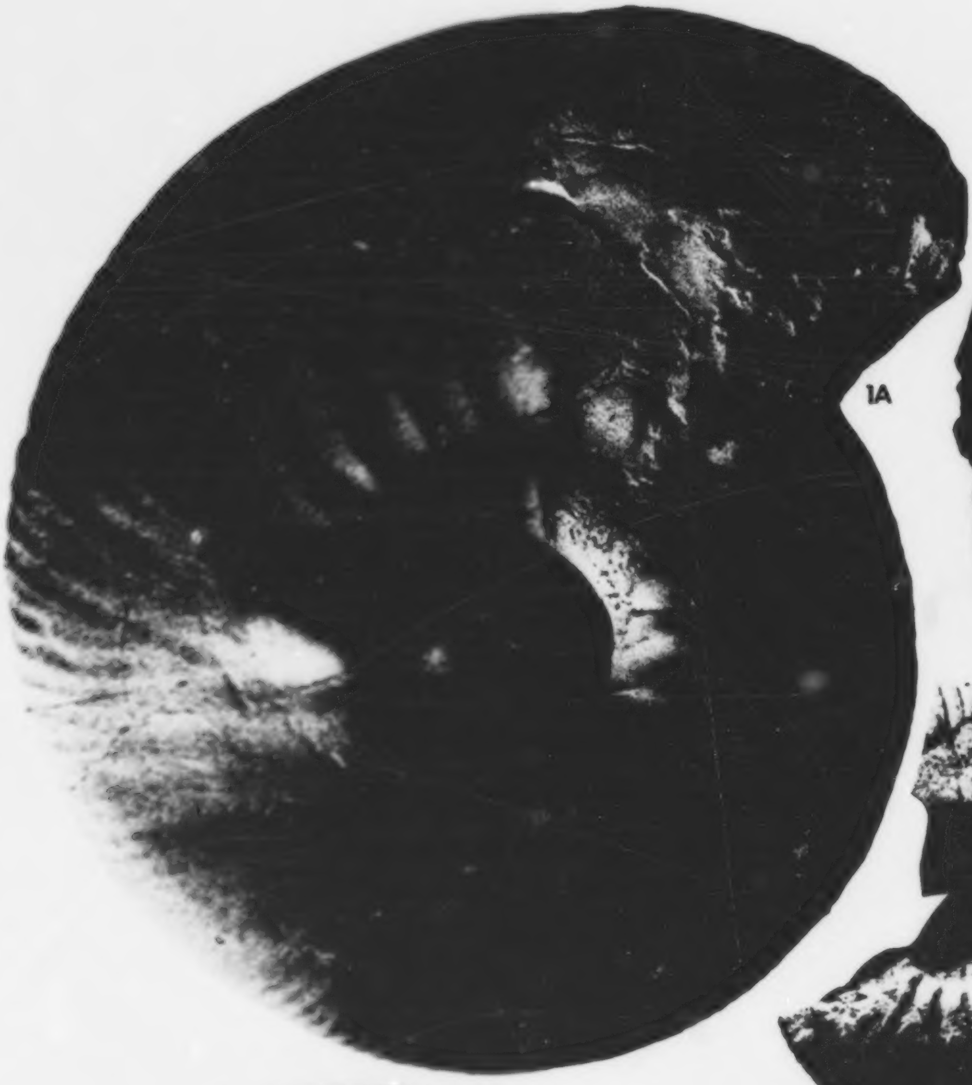
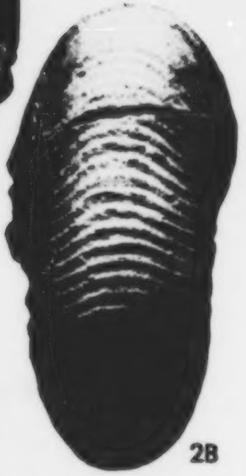

1A
1B
2B
2A

Plate 18

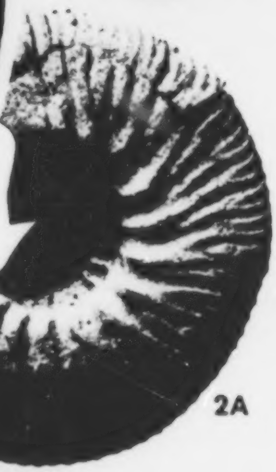
Figures 1A, 1B.	*Prodichotomites flexicosta* (Koenen, 1902). Zone of *Prodichotomites hollwedensis*, basal upper Valanginian. Twiehausen, Northwest Germany. BGR, kv 122, Hannover. An adult living chamber with a weakened sculpture (especially on the flanks), x 1. 1A. Lateral view; 1B. Terminal cross-section and ventral view of the early half of the whorl.
Figures 2A, 2B.	*Prodichotomites polytomus* (Koenen, 1902). Upper Valanginian. Wiedenbruegge, Northwest Germany. BGR, kv 143, Hannover. The specimen is distorted and belongs to an atypically sculptured variant, x1. 2A. Lateral view; 2B. Ventral view.



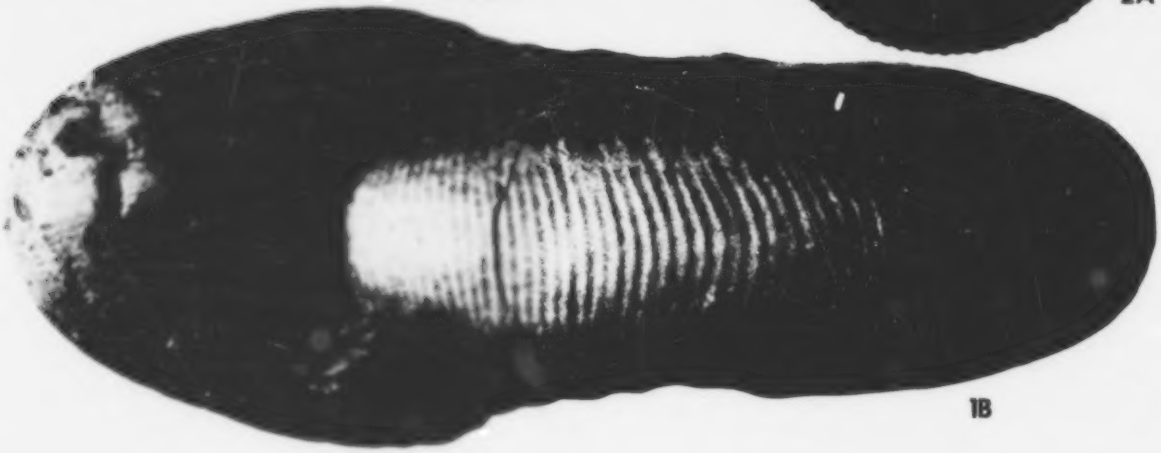
1A



2B



2A



1B

Plate 19

Figures 1A, 1B. *Prodichotomites glaber* n. sp. Upper Valanginian. Hasslage-Nord, Northwest Germany. BGR, kv 144, Hannover. An entirely septate fragment, x 1. 1A. Ventral view; 1B. Lateral view.

Figures 2A-2C. *Prodichotomites polytomus* (Koenen, 1902). Lower upper Valanginian. Hollwede, Northwest Germany. BGR, kv 288, Hannover. A typical specimen, x 1. 2A. Lateral view; 2B. Terminal cross-section and ventral view of the early half of the whorl; 2C. Lateral view of the other flank.

Figures 3A, 3B. *Euryptychites diplotomus* (Koenen, 1902). *Platylenticeras*-Beds, lower lower Valanginian. Sachsenhagen, Northwest Germany. BGR, kv 253, Hannover. A fine ribbed variant that features fasciculate bundles, x 1, 3A. Lateral view; 3B. Ventral view of the oral part of the whorl.

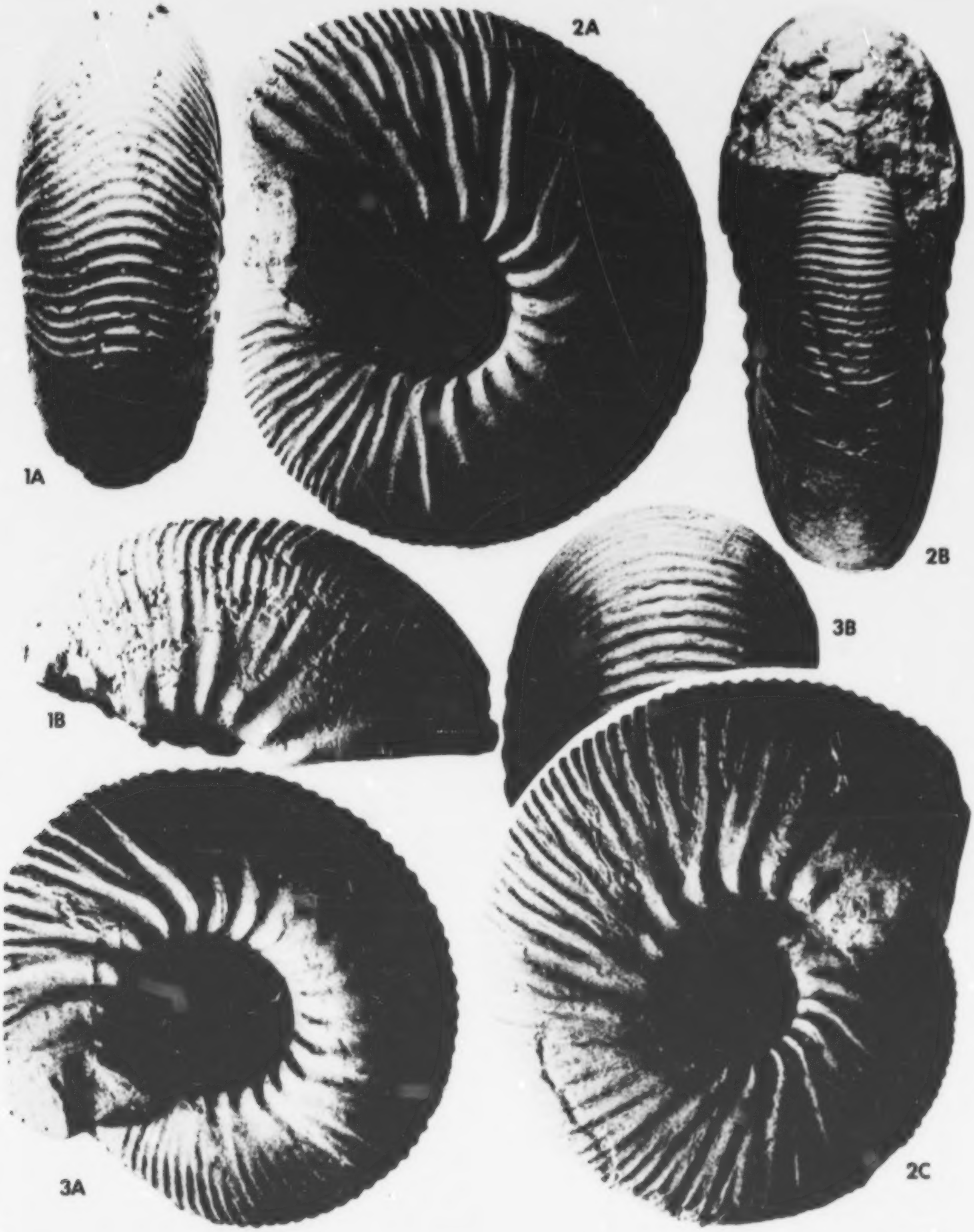
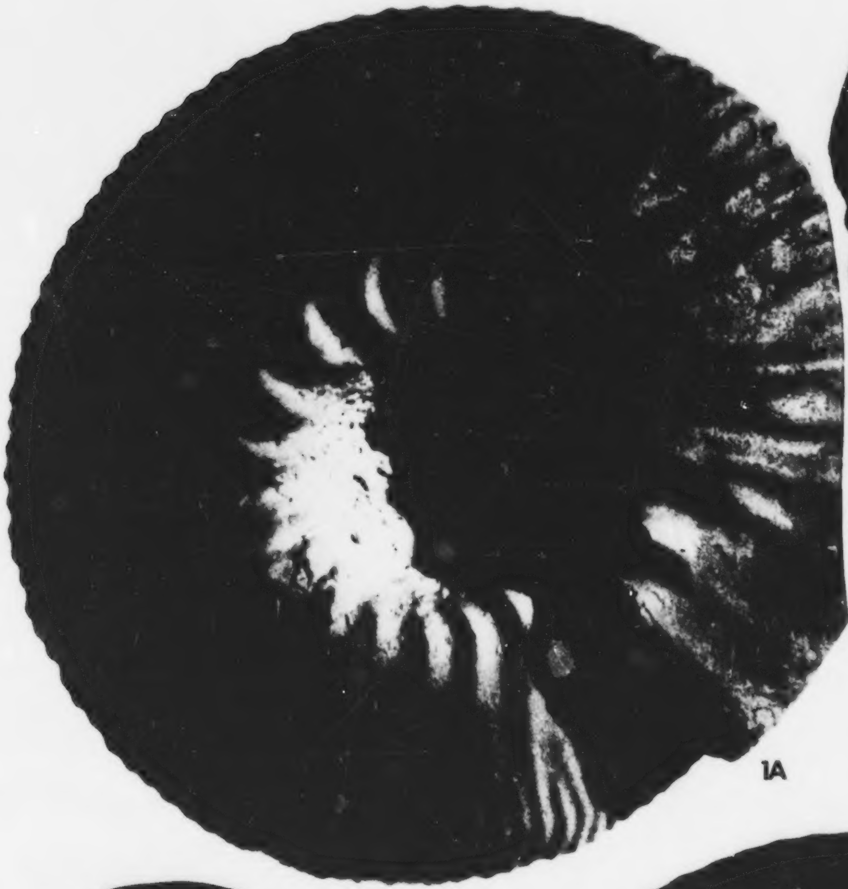

1A
2A
2B
1B
3B
3A
2C

Plate 20

Figures 1A, 1B.	*Prodichotomites polytomus* (Koenen, 1902). Lower upper Valanginian. Hollwede II, Northwest Germany. BGR, kv 126, Hannover. A presumably adult living chamber, x 1. 1A. Lateral view; 1B. Ventral view of the early part of the whorl.
Figures 2A, 2B.	*Prodichotomites glaber* n. sp. Lower upper Valanginian. Hollwede II, Northwest Germany. BGR, kv 302, Hannover. A half-whorl fragment of an intermediate living chamber. The specimen belongs to a variant with an obtuse venter, x 1. 2A. Ventral view; 2B. Lateral view.
Figure 3.	*Prodichotomites complanatus* (Koenen, 1902). Lower shale member of "*Dichotomites*-Beds", lower upper Valanginian. Borehole Nordhorn Nord 9, core at 584 m level below top, Northwest Germany. BGR, kv 251, Hannover. A strongly laterally deformed juvenile shell, x 1.
Figure 4.	*Prodichotomites complanatus* (Koenen, 1902). "*Dichotomites*-Beds", upper Valanginian. Borehole Nordhorn Nord 5, core at 387 m level below top, Northwest Germany. BGR, kv 252, Hannover. A strongly laterally deformed fragment of a juvenile shell, x 1.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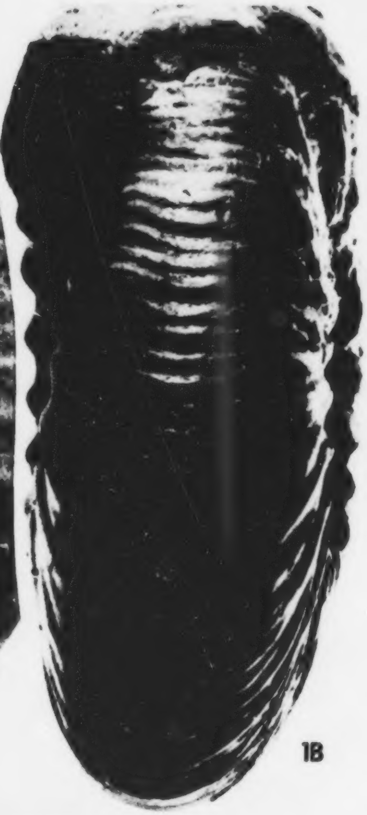
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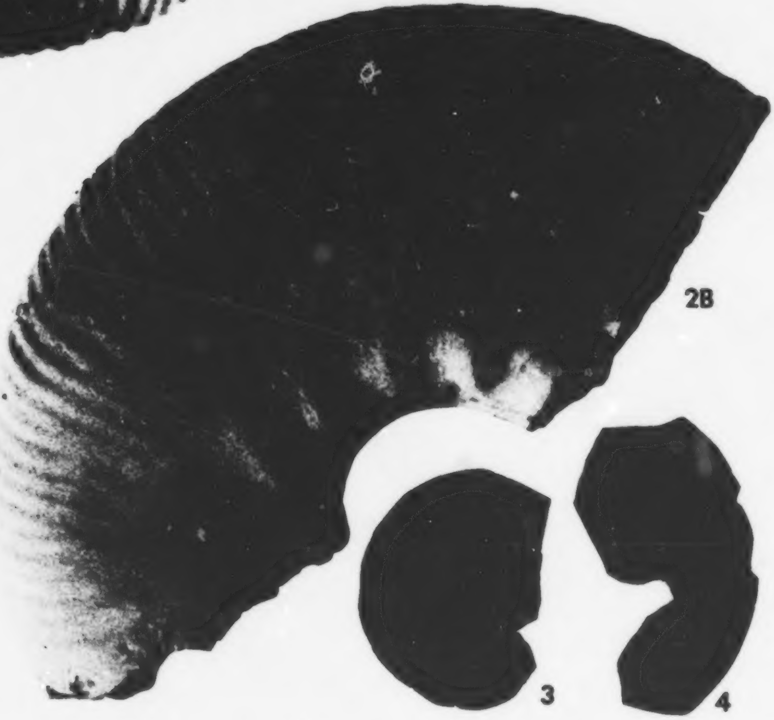
2B

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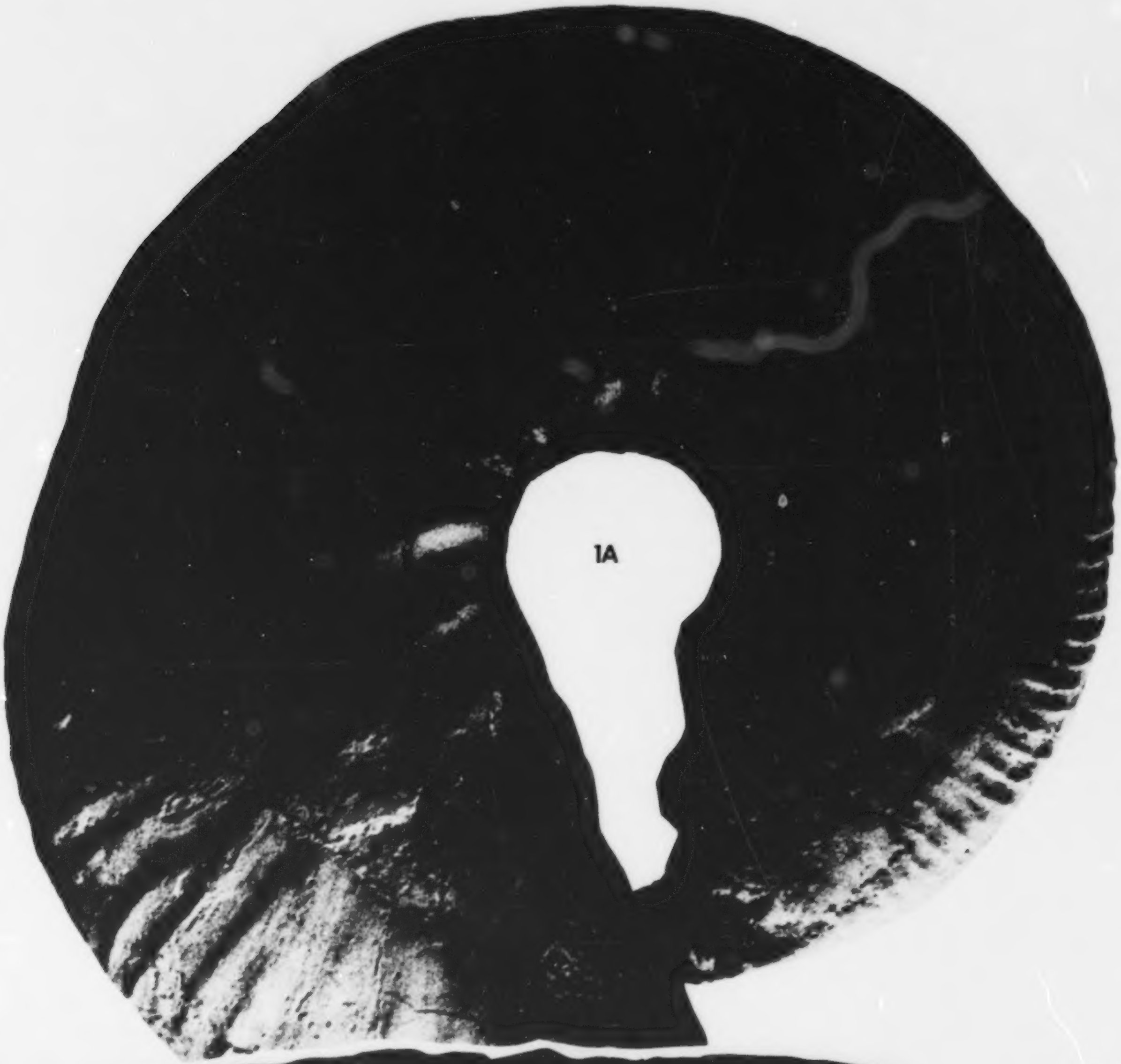
Plate 21

Figures 1A, 1B. *Prodichotomites glaber* n. sp. Lower upper Valanginian. Hollwede II, Northwest Germany. BGR, kv 303, Hannover. An adult living chamber, x 1. 1A. Lateral view; 1B. Ventral view of the early half of the whorl.



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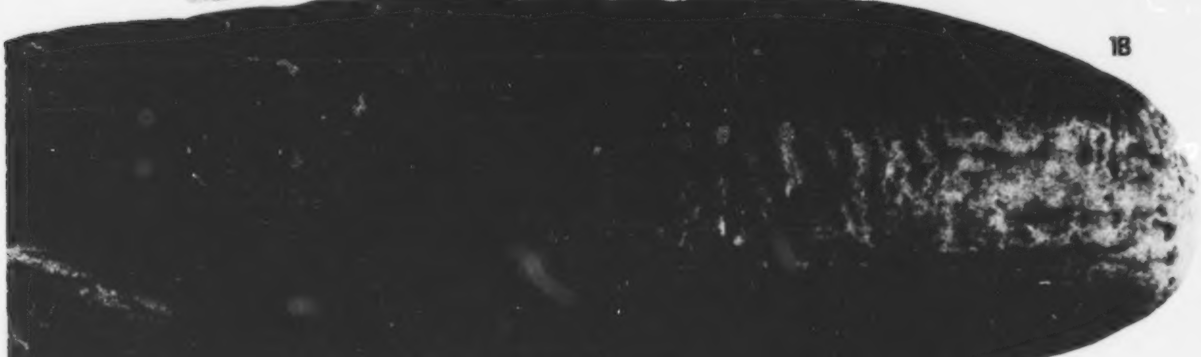
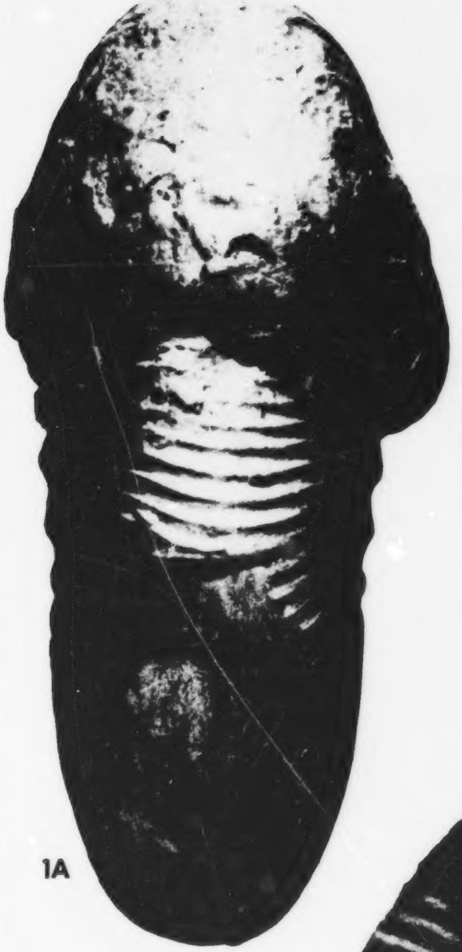


1B

Plate 22

Figures 1A-1C. *Prodichotomites glaber* n. sp. Holotype. Lower upper Valanginian. Hollwede II, Northwest Germany. BGR, kv 305, Hannover. A presumably late intermediate whorl, x 1. 1A. Ventral view of the early part of the whorl and its terminal cross-section; 1B. Lateral view; 1C. Lateral view of the other flank.

Figure 2. *Prodichotomites flexicosta* (Koenen, 1902). Zone of *Prodichotomites hollwedensis*, basal upper Valanginian. Twiehausen, Northwest Germany. BGR, kv 295, Hannover, x 1. A poorly preserved juvenile shell. See Pl. 16, fig. 2, for its ventral view.



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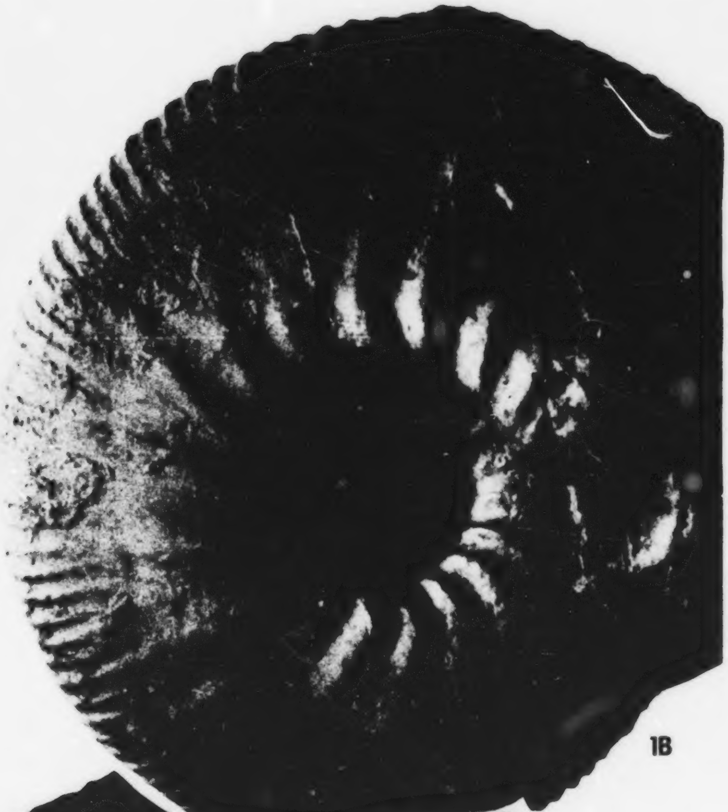

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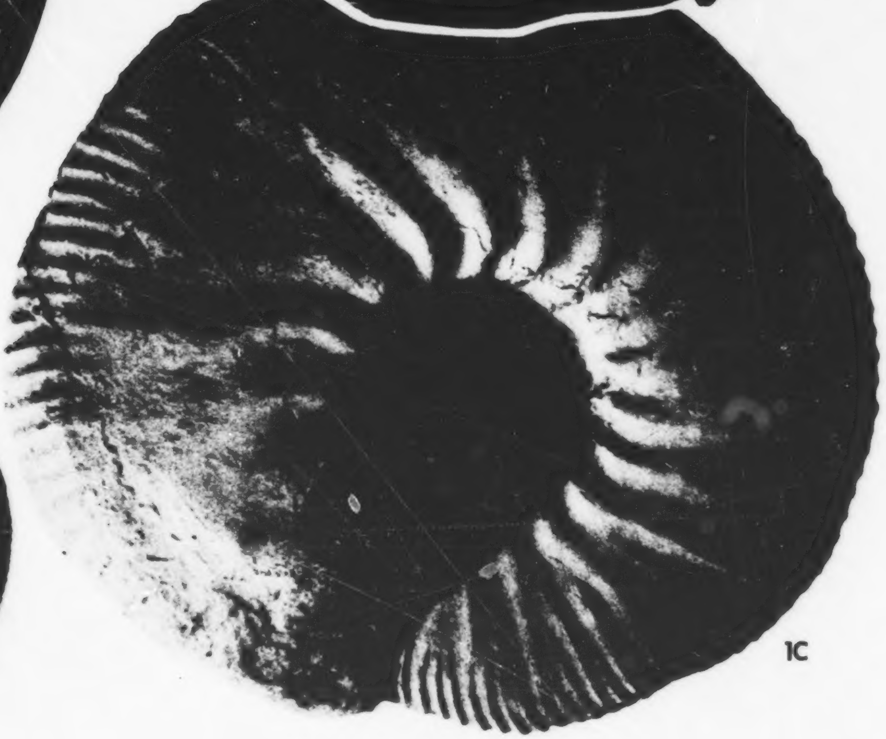


1C

2

Plate 23

Figures 1A, 1B. Transitional form connecting *Prodichotomites perovalis* (Koenen, 1902) with *P. ivanovi* (Aristov, 1974). Upper upper Valanginian. Ottensen, Northwest Germany. BGR, kv 130, Hannover. An intermediate whorl, x 1. 1A. Lateral view; 1B. Ventral view of adoral half of the whorl.

Figures 2A-2C. *Prodichotomites perovalis* (Koenen, 1902). Upper Valanginian. Hasslage-Nord, Northwest Germany. BGR, kv 127, Hannover. A representative of the typical variant, x 1. 2A. Lateral view; 2B. Lateral view of the other flank; 2C. Terminal cross-section and ventral view of the early half of the whorl.

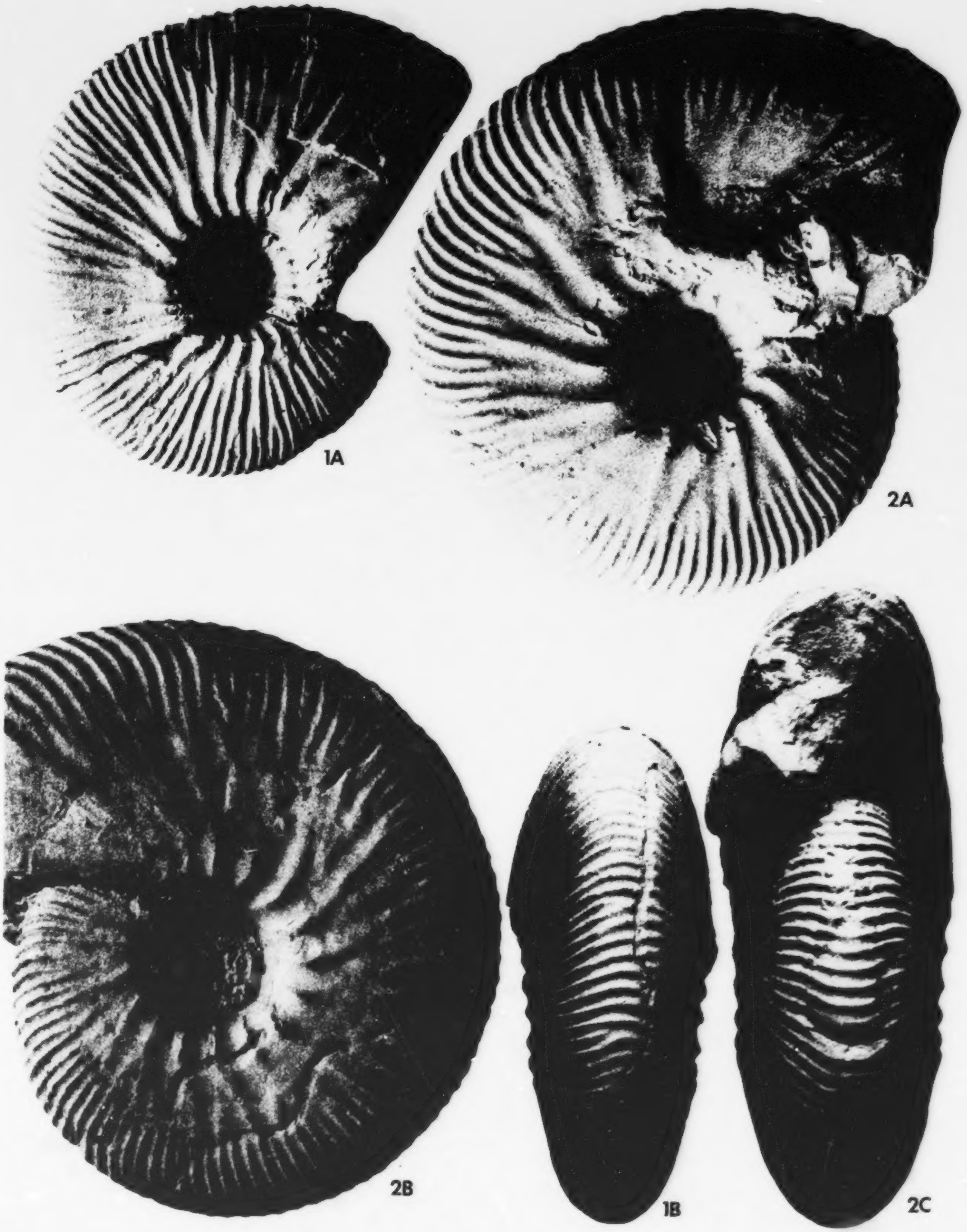
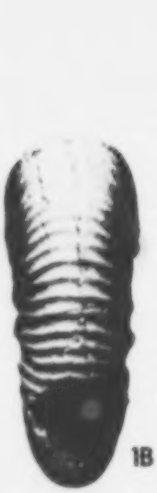

1A
2A
2B
1B
2C

Plate 24

Figures 1A-1C.	*Polyptychites oerlinghusanus* (Weerth, 1884). Lower(?) *Polyptychites*-Beds, middle part of lower Valanginian. Bueckeburg-Jetenburg, Northwest Germany. BGR, kv 263, Hannover. An adult specimen, x 1. 1A. Lateral view; 1B. Ventral view of the oral half of the whorl; 1C. Terminal cross-section and ventral view of the early half of the whorl.
Figures 2; 3A, 3B; 4A, 4B.	*Prodichotomites ivanovi* (Aristov, 1974). Upper upper Valanginian. Ottensen, Northwest Germany. All photos x 1. Fig. 2: BGR, kv 308, Hannover. An entirely septate, fragmentary specimen that exhibits well the characteristic features of the species. Figs. 3A, 3B: BGR, kv 309, Hannover. An entirely septate specimen that exhibits the early to intermediate growth stages. 3A. Lateral view; 3B. Terminal cross-section and ventral view of the early half of the whorl. Figs. 4A, 4B. BGR, kv 311, Hannover. A fragmentary, juvenile shell. 4A. Lateral view; 4B. Ventral view.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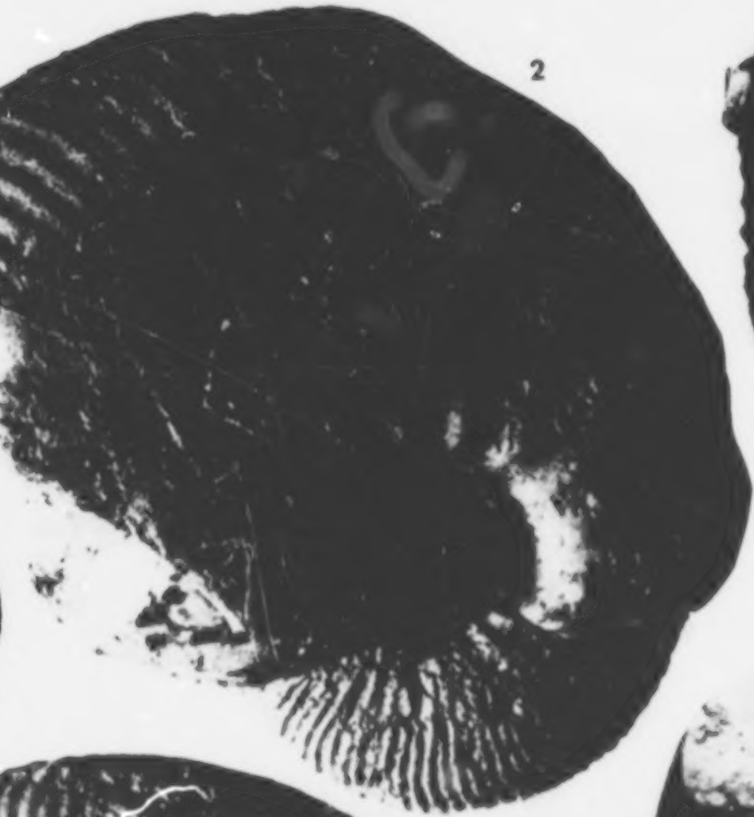
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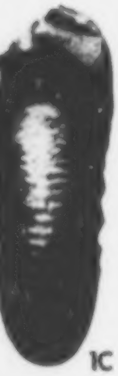
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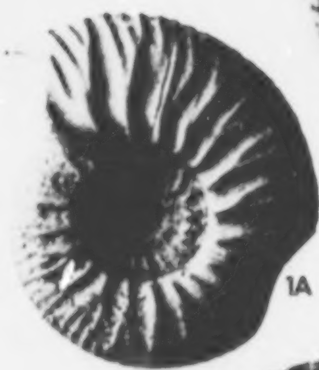
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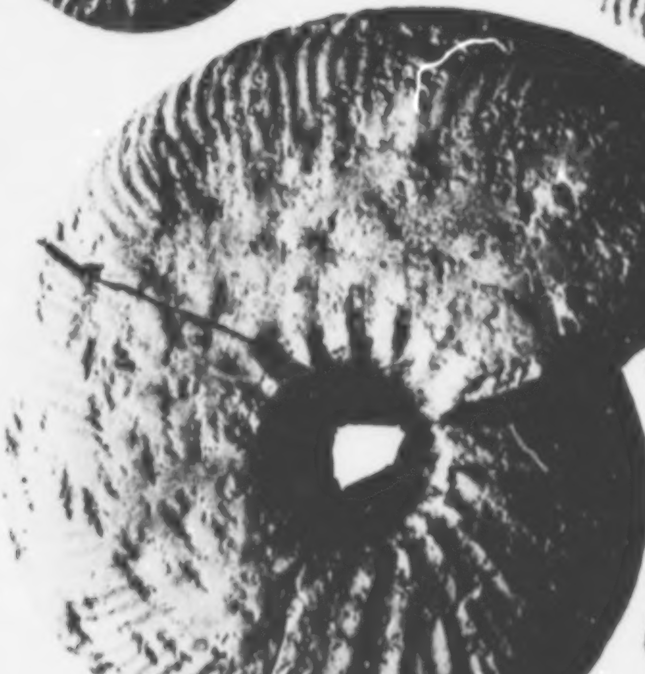
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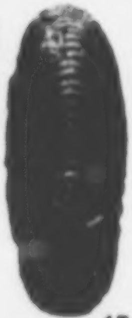
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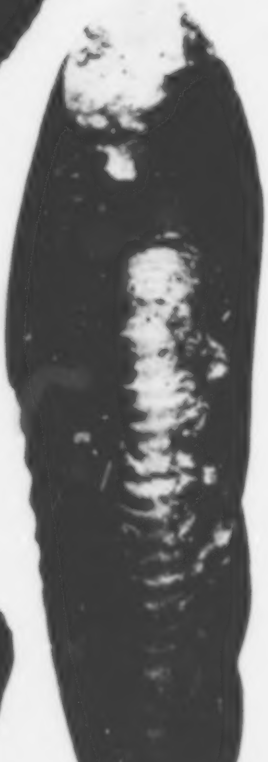
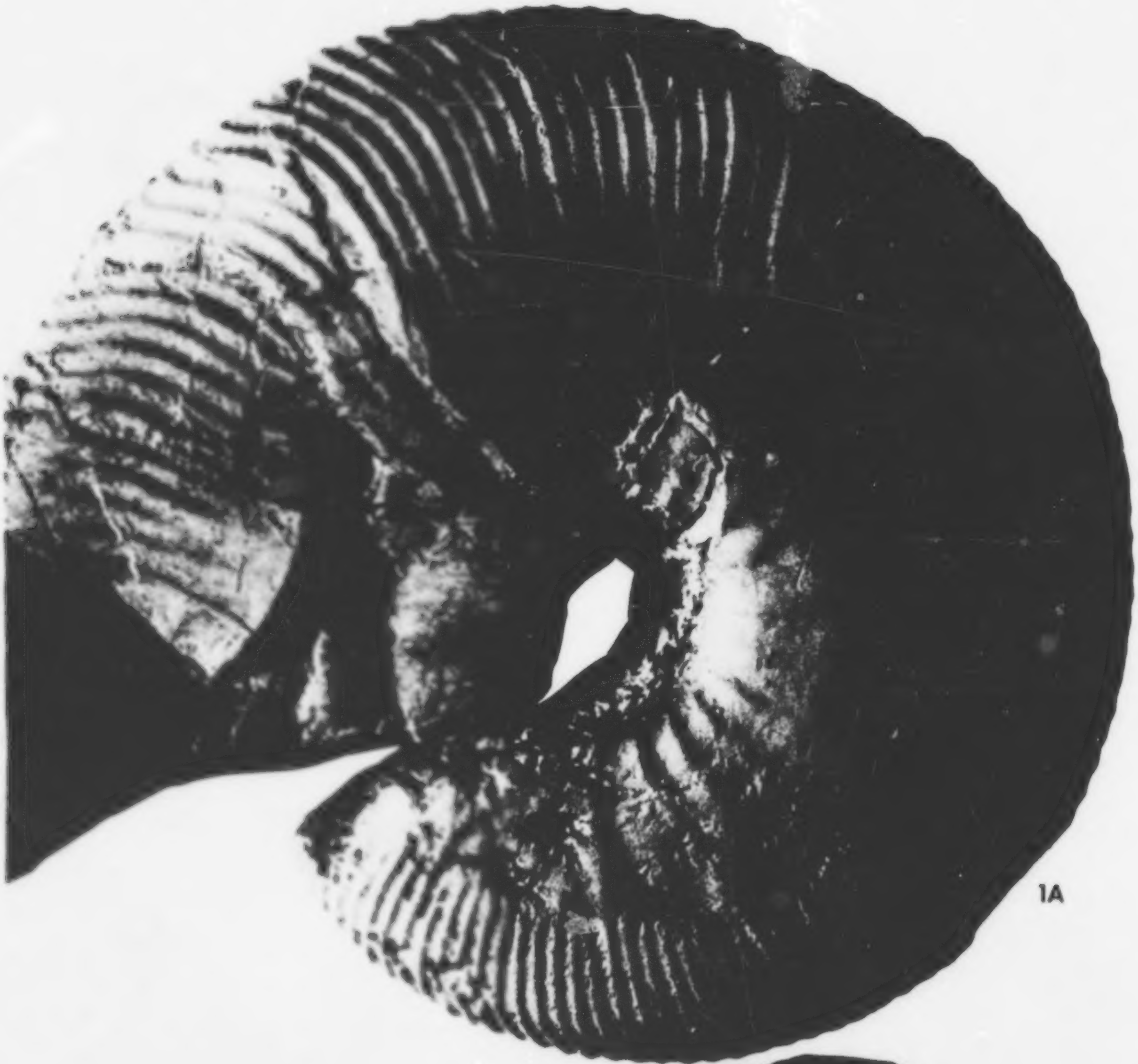

3B

4A

Plate 25

Figures 1A, 1B *Prodichotomites ivanovi* (Aristov, 1974). Upper upper Valanginian. Ottensen, Northwest Germany. BGR, kv 310, Hannover. Oralmost whorl of an adult specimen that consists predominantly of the living chamber, x 1. 1A. Lateral view; 1B. Ventral view of the early part of the whorl.



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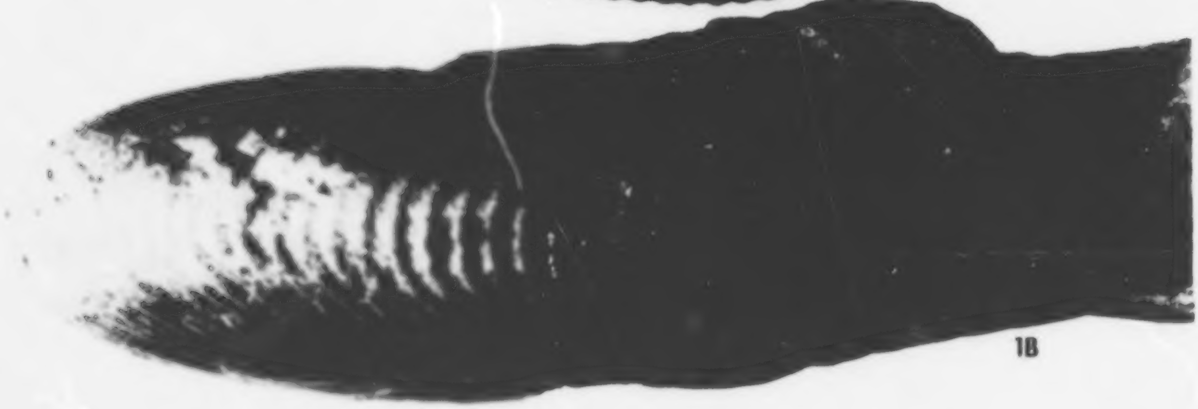


1B

Plate 26

Figure 1. *Euryptychites latissimus* (Neumayr and Uhlig, 1881). Upper *Platylenticeras*-Beds, lower lower Valanginian. Sachsenhagen, Northwest Germany. BGR, kv 334, Hannover. The last quarter of the last preserved whorl of this exceptionally well preserved specimen is the adult living chamber, x 1. See Pl. 27, fig. 1 for the ventral view.

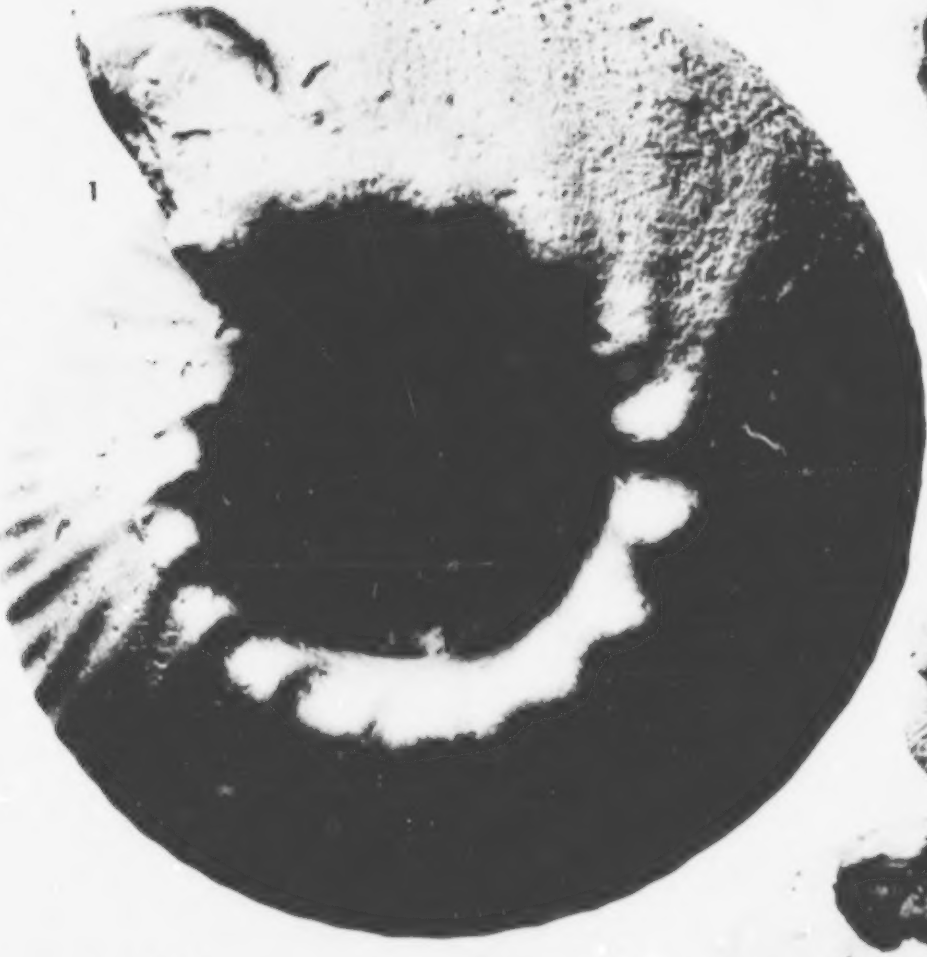
Figures 2A, 2B. *Polyptychites keyserlingi* (Neumayr and Uhlig, 1881). *Polyptychites*-Beds, lower Valanginian. Bueckeburg-Jetenburg, Northwest Germany. BGR, kv 340, Hannover. A juvenile shell, x 1. 2A. Lateral view; 2B. Ventral view of the oral half of the whorl.

Figures 3A, 3B. *Paratollia kemperi* Casey, 1973. Lowermost *Polyptychites*-Beds, middle part of lower Valanginian. Bueckeburg-Jetenburg, Northwest Germany. BGR, kv 351, Hannover. A poorly preserved and completely septate specimen that represents juvenile to intermediate growth stages, x 1. 3A. Lateral view; 3B. Terminal cross-section and ventral view of the early half of the whorl.

Figure 4. *Euryptychites latissimus* (Neumayr and Uhlig, 1881). *Polyptychites*-Beds, lower Valanginian. Bueckeburg-Jetenburg, Northwest Germany. BGR, kv 369, Hannover. An entirely septate, juvenile shell; its rib bundles are almost fasciculate (see Figure 14c for suture line). Lateral view, x 1. See Pl. 27, fig. 4 for the ventral view.

Figures 5A, 5B. *Polyptychites keyserlingi* (Neumayr and Uhlig, 1881). *Polyptychites*-Beds, lower Valanginian. Bueckeburg-Jetenburg, Northwest Germany. BGR, kv 372, Hannover. A juvenile shell, x 1. 5A. Lateral view; 5B. Terminal cross-section and ventral view of the early half of the whorl.

Figure 6. *Euryptychites* aff. *E. laevis* Donovan, 1953. Ventral view of specimen reproduced in Pl. 28, fig. 1, x 1.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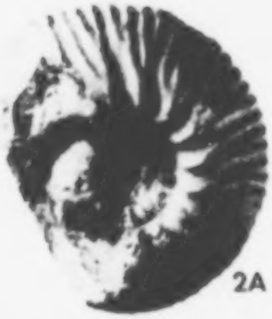
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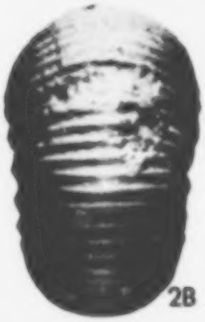
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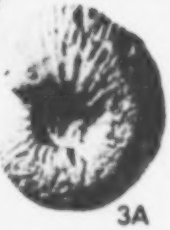
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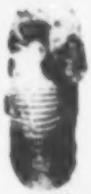
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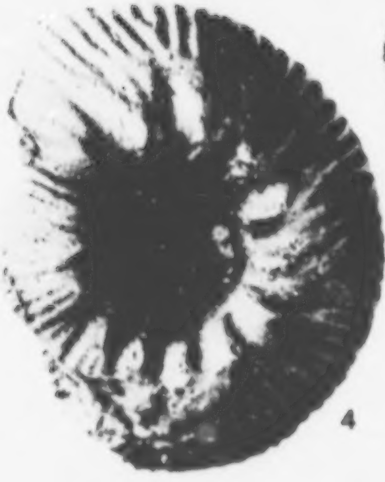
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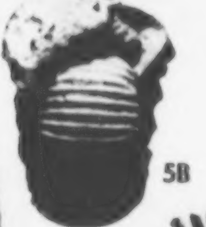
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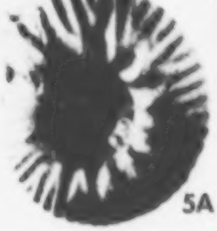
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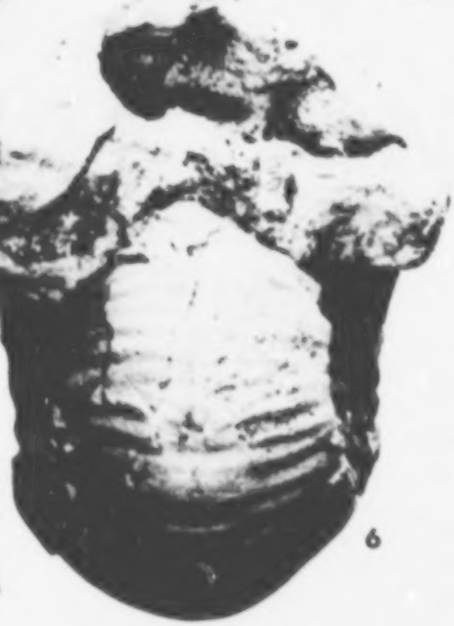
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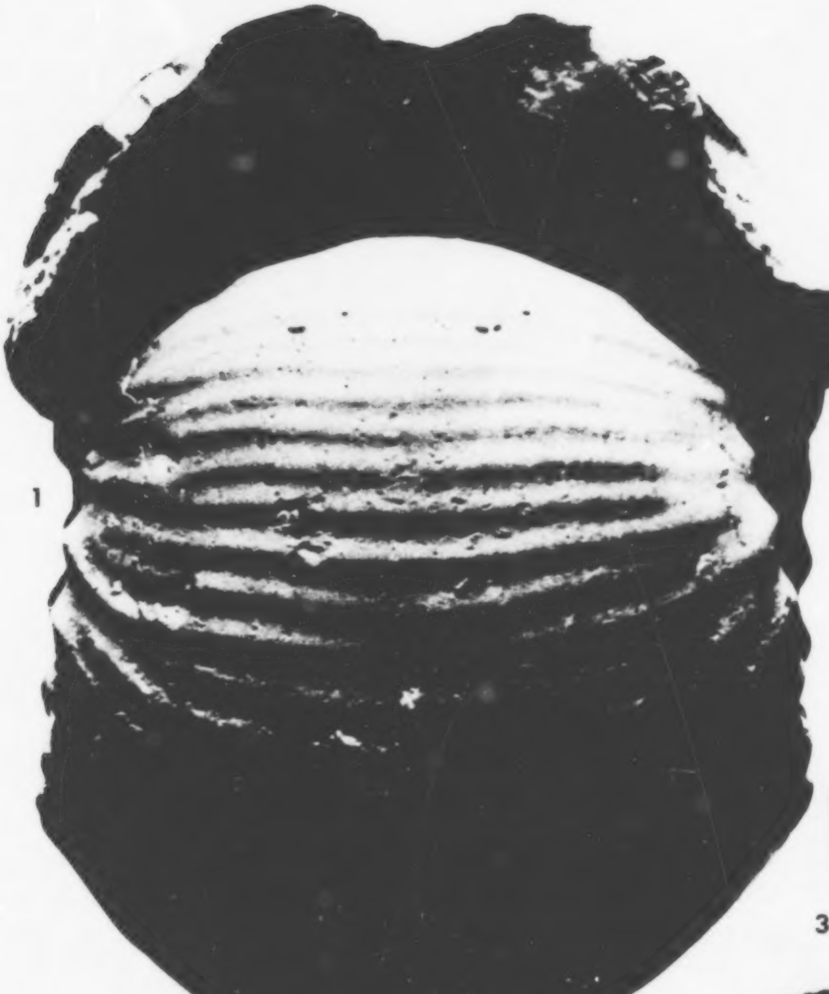
Plate 27

Figure 1.	*Euryptychites latissimus* (Neumayr and Uhlig, 1881). Ventral view of the specimen reproduced in Pl. 26, fig. 1, x 1.
Figure 2.	*Prodichotomites hollwedensis* Kemper, 1978. Ventral view of the specimen reproduced in Pl. 28, fig. 4, x 1.
Figures 3A-3C.	*Bodylevskites pumilio* (Vogel, 1959). Lowermost *Polyptychites*-Beds, lower Valanginian. Bueckeburg-Jetenburg, Northwest Germany. BGR, kv 360, Hannover. 3A. Lateral view, x 1. 3B. The same, x 1.5; 3C. Ventral view, x 2.
Figure 4.	*Euryptychites latissimus* (Neumayr and Uhlig, 1881). Terminal cross-section and ventral view of the early part of the whorl of the specimen reproduced in Pl. 26, fig. 4, x 1.
Figures 5A, 5B.	*Polyptychites pavlowi* Koenen, 1902. *Polyptychites*-Beds, lower Valanginian. Bueckeburg-Jetenburg, Northwest Germany. BGR, kv 65, Hannover, x 1. See Pl. 4, fig. 4, for the ventral view. 5A. Lateral view of the fragmentary earlier whorls; 5B. Lateral view of the next older whorl fragment.
Figure 6.	*Euryptychites* aff. *E. laevis* Donovan, 1953. Lower *Polyptychites*-Beds, lower Valanginian. Bueckeburg-Jetenburg, Northwest Germany. BGR, kv 363, Hannover. Lateral view, x 1. See Pl. 28, fig. 1 for the lateral view of the other flank and Pl. 26, fig. 6 for the ventral view.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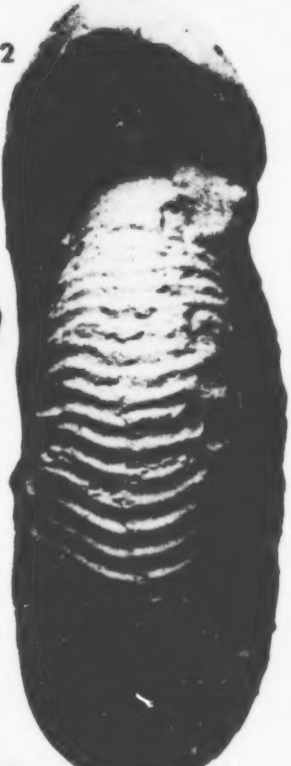
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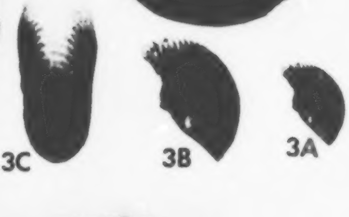
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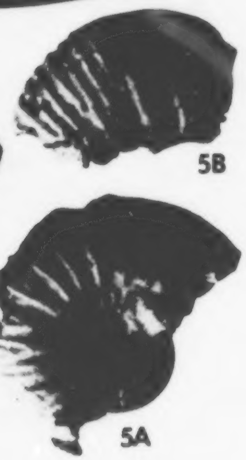
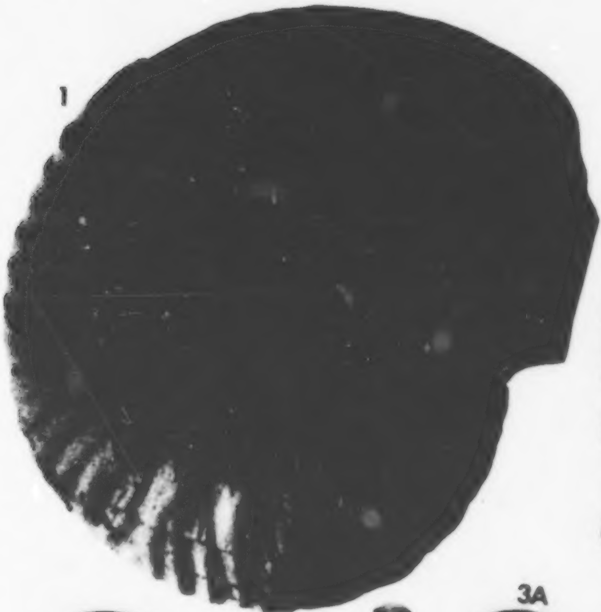

5B 5A

6

Plate 28

Figure 1.	*Euryptychites* aff. *E. laevis* Donovan, 1953. The other lateral view of the specimen reproduced in Pl. 26, fig. 6 and Pl. 27, fig. 6, x 1.
Figure 2.	*Polyptychites hapkei* n. sp. Ventral view of the holotype, x 1. Lateral view is reproduced in Pl. 10, fig. 3.
Figure 3A-3C.	*Bodylevskites pumilio* (Vogel, 1959). Lowermost *Polyptychites*-Beds, middle part of the lower Valanginian. Bueckeburg-Jetenburg, Northwest Germany. BGR, kv 356, Hannover. 3A. Lateral view, x 1; 3B. The same, x 1.5. Note the constriction; 3C. Ventral view, x.1.
Figure 4.	*Prodichotomites hollwedensis* Kemper, 1978. Lower upper Valanginian. Hollwede, Northwest Germany. BGR, kv 115, Hannover. Lateral view, x 1. See Pl. 27, fig. 2, for the ventral view.
Figure 5A, 5B.	*Polyptychites* juven. cf. *P. pavlowi* Koenen, 1902. *Polyptychites*-Beds, lower Valanginian. Bueckeburg-Jetenburg, Northwest Germany. BGR, kv 373, Hannover. 5A. Lateral view of an early whorl; 5B. Lateral view of the next following early whorl. Both photographs made from plaster casts, x 1. An example of the early development of sculpture in *Polyptychites*.
Figures 6, 7.	*Bodylevskites pumilio* (Vogel, 1959). Age and locality as for the Figure 3, which see for further details. Fig. 6: BGR, kv 357, Hannover. Lateral view, x 1. Figs. 7A, 7B: BGR, kv 352, Hannover. 7A. Lateral view, x 1; 7B. The same view as last, x 1.5.

1



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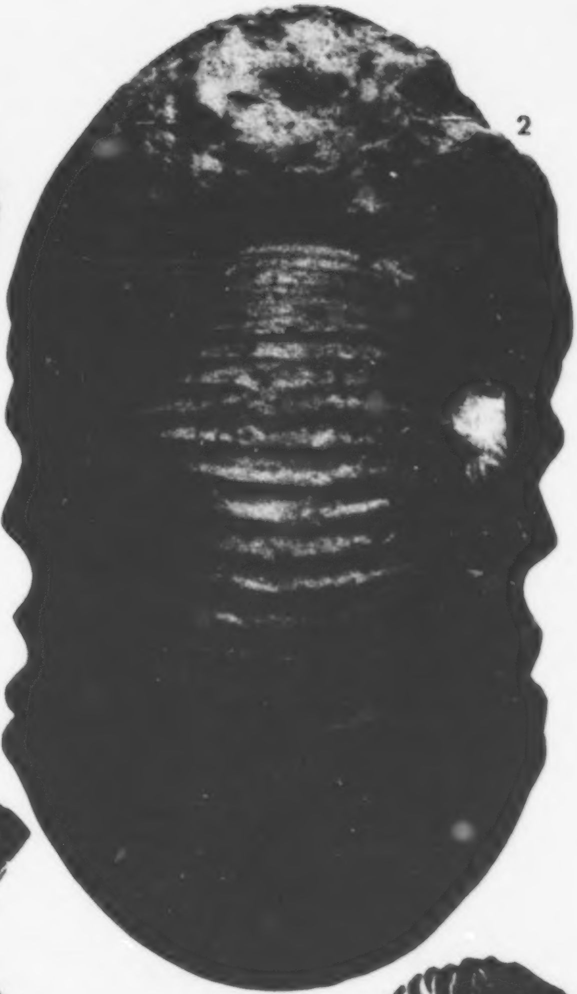

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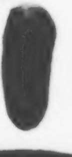
3C



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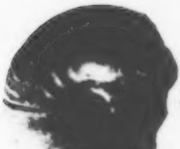

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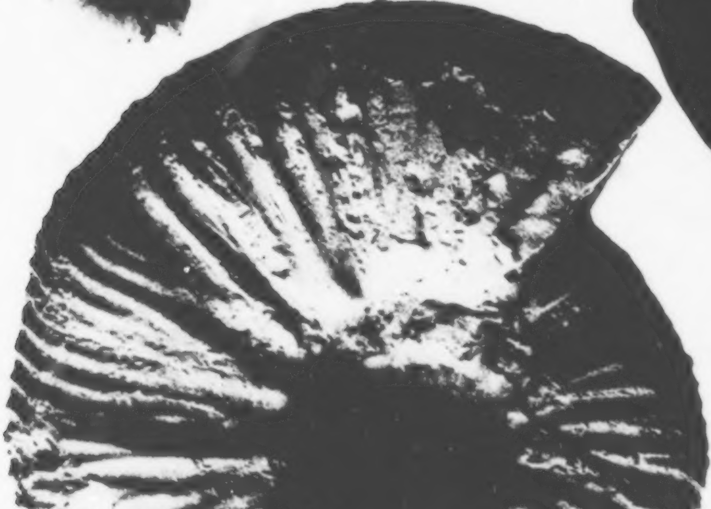

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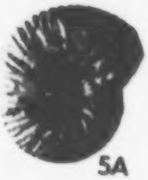

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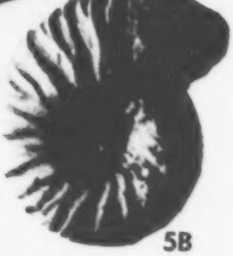

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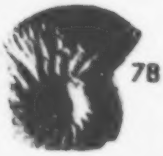

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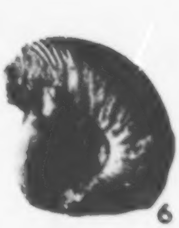

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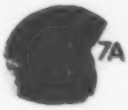
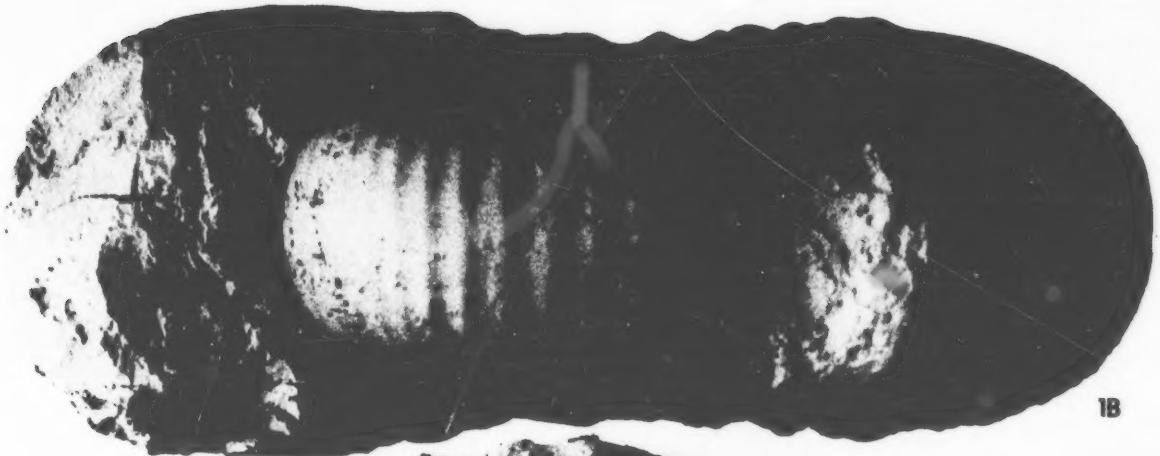


Plate 29

Figures 1A, 1B. *Polyptychites clarkei* Koenen, 1909. *Polyptychites*-Beds, upper lower Valanginian. Lindhorst, Northwest Germany. BGR, kv 88, Hannover. A morphologically typical, completely preserved specimen, x 1. 1A. Lateral view; 1B. Terminal cross-section and ventral view of the early half of the whorl.



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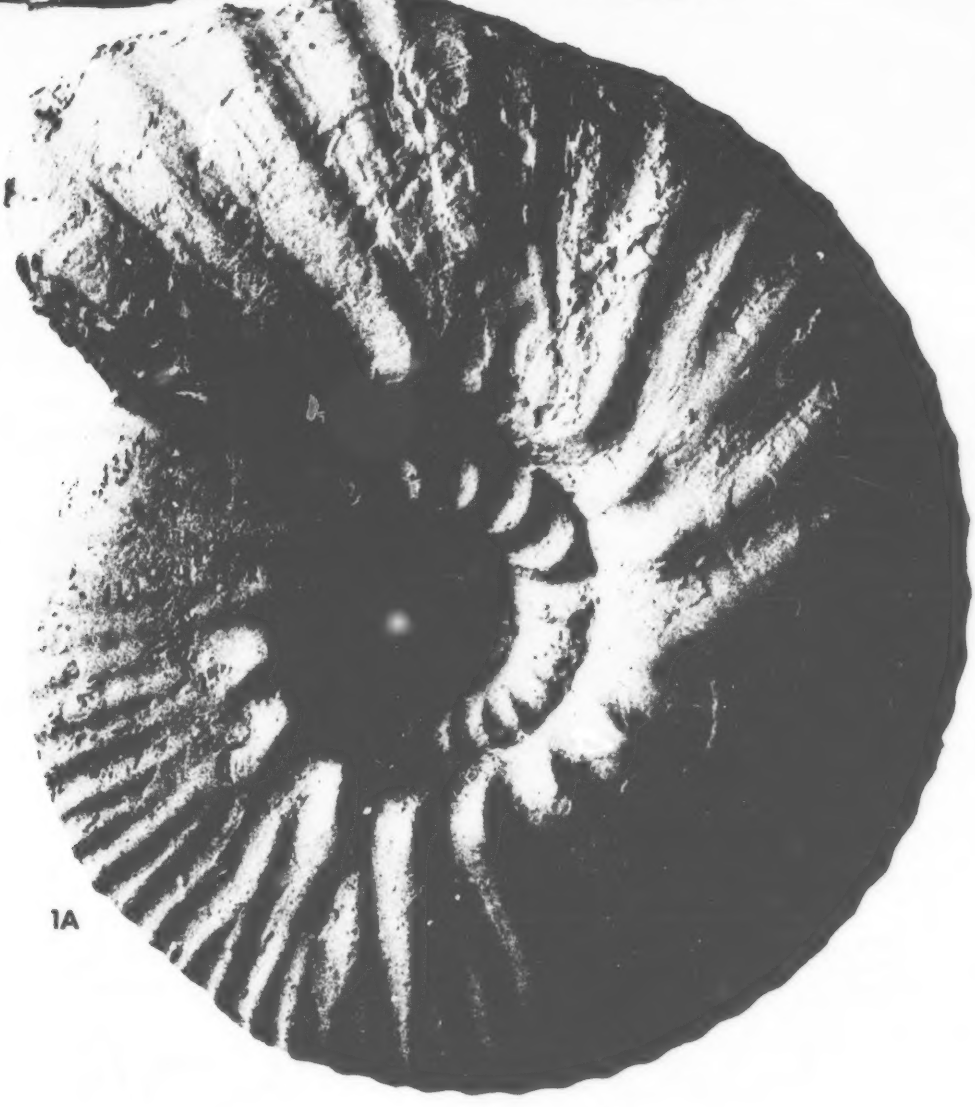


1A

Plate 30

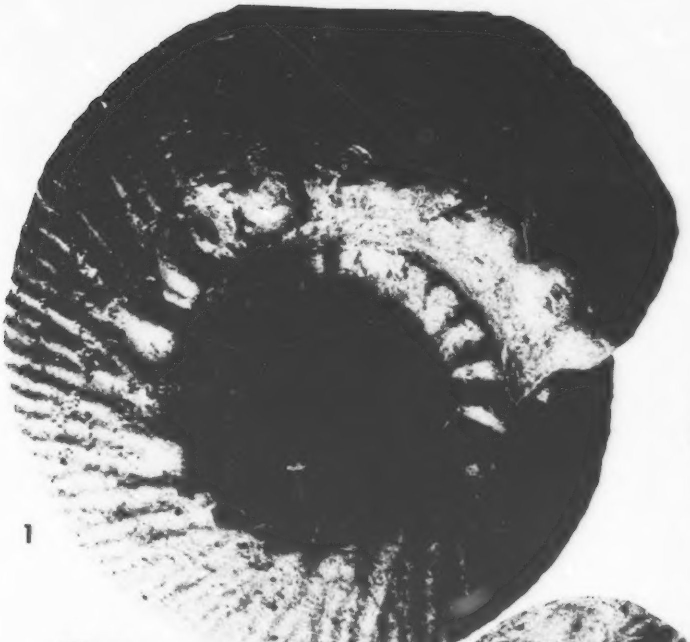
Figures 1; 2A, 2B; 3A, 3B. *Hollwediceras sphaericus* (Koenen, 1902). Basal upper Valanginian. Hollwede, Northwest Germany. All specimens are completely septate phragmocones. Therefore, they only represent early to intermediate growth stages. All photographs, x 1.

Fig. 1: BGR, kv 365, Hannover. A specimen combining a great number of ribs per whorl with a rather irregular mode of bundling. However, it exhibits tridichotomous rib bundles on the penultimate whorl.

Figs. 2A, 2B: BGR, kv 366, Hannover. A variant that exhibits particularly clearly the strongly adventrally displaced branching points. However, the figured growth stages of this specimen exhibit predominantly bidichotomous rib bundles. 2A. Lateral view; 2B. Ventral view.

Figs. 3A, 3B: BGR, kv 364, Hannover. The variant with the widest and therefore most *Euryptychites*-like cross-section. 3A. Cross-sections of two whorls and the ventral view of the early third of the inner whorl; 3B. Lateral view of the same.

Figure 4. *Polyptychites canadensis* Kemper and Jeletzky, 1979. Ventral view of the holotype, x 1. See description of Pl. 31, figs. 1A, 1B for further details.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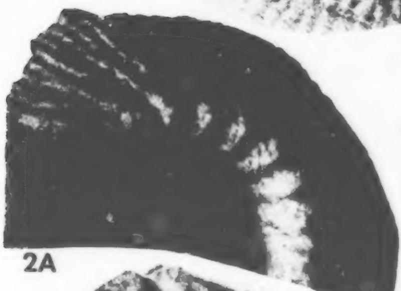
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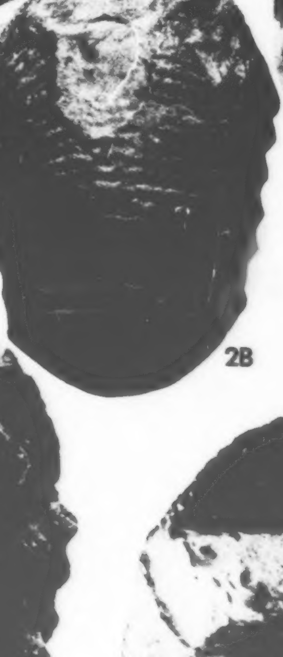
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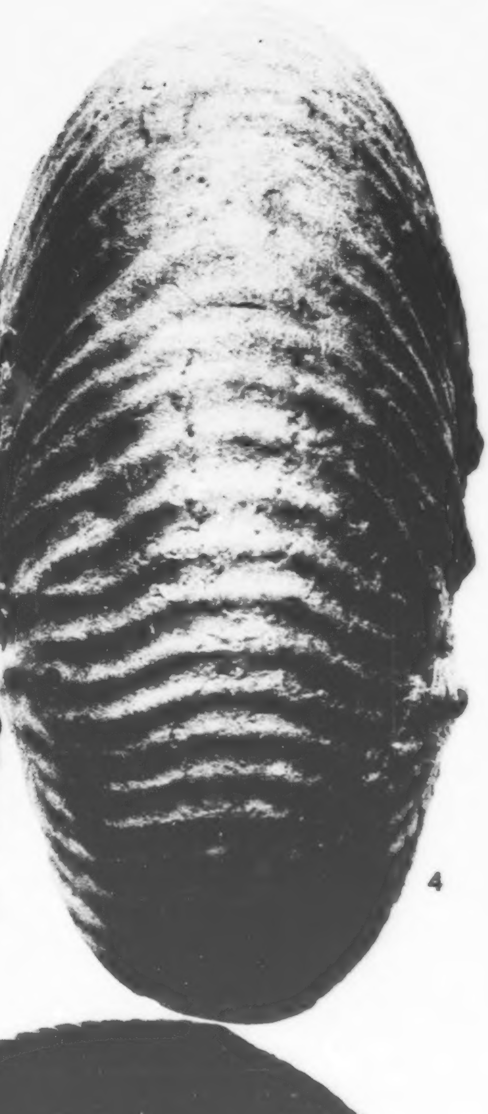
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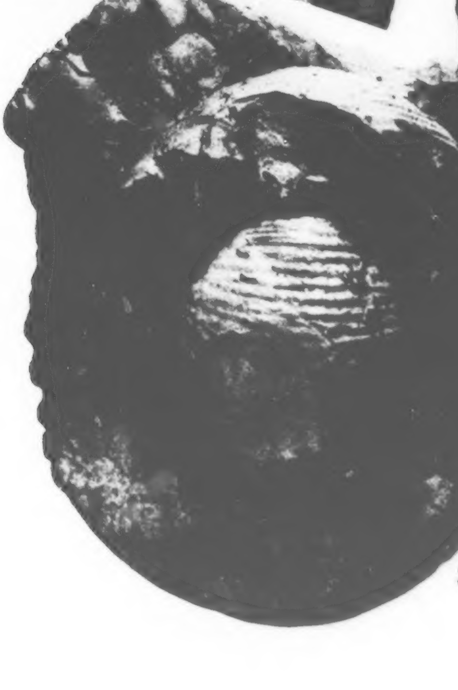
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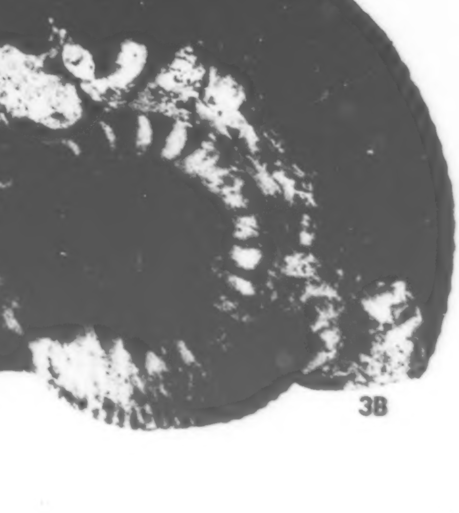

3B

Plate 31

Figures 1A, 1B. *Polyptychites canadensis* Kemper and Jeletzky, 1979. Holotype. GSC 61755, GSC loc. 93866. An entirely septate, fragmentary shell, x 1. 1A. Lateral view; 1B. Cross-section of three intermediate whorls. See Pl. 30, fig. 4 for the ventral view of the oralmost preserved whorl.

Figures 2A-2C. *Siberiptychites* (*Pseudoeuryptychites*) *middendorffi* (Pavlow, 1914). Adult external suture line of the specimen GSC 77102 reproduced in Pl. 36, figs. 2A, 2B. All photographs, x 1. 2A. First and second lateral lobes; 2B. Second lateral lobe, second lateral saddle and the first auxiliary lobe; 2C. First to third auxiliary lobes. See Figure 56a for the reproduction of the entire suture line.

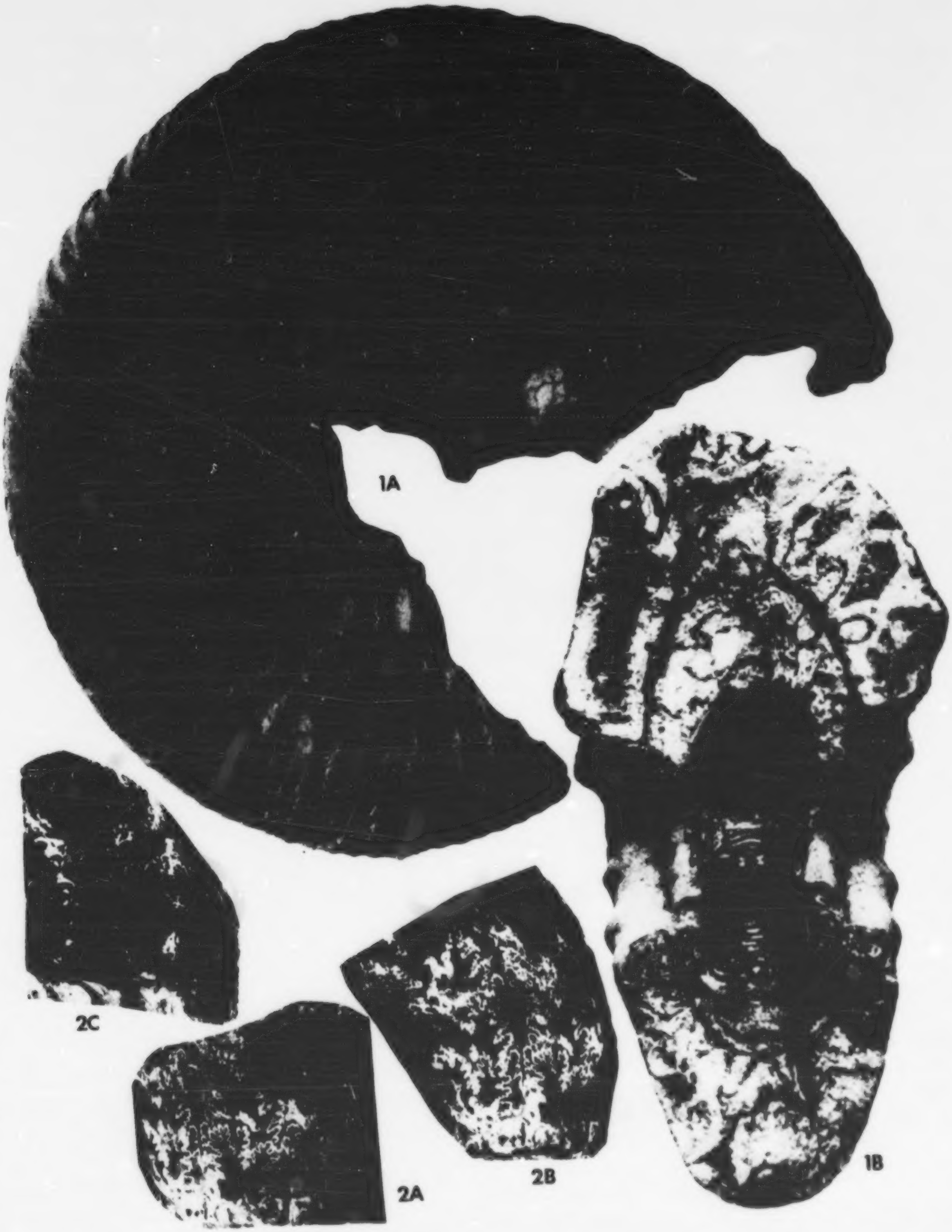
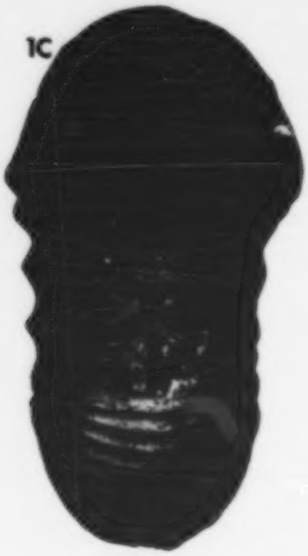

1A
1B
2C
2A
2B

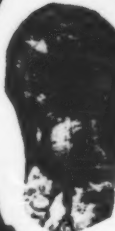
Plate 32

Figures 1A-1C.	*Polyptychites keyserlingi* (Neumayr and Uhlig, 1881). GSC 32592, GSC loc. 82695. A presumably adult specimen that includes most (about three-quarters of the last whorl) of the living chamber, x 1. 1A. Lateral view; 1B. Ventral view; 1C. Terminal cross-section and the ventral view of the early part of the last whorl.
Figures 2A-2D.	*Polyptychites keyserlingi* (Neumayr and Uhlig, 1881). GSC 77095, GSC loc. 82695. A presumably adult specimen that includes much (about two-fifths of the last whorl) of the lviing chamber. Phragmocone is strongy deformed, x 1. 2A. Lateral view; 2B. Ventral view; 2C. Terminal cross-section and ventral view of the strongly deformed early part of the whorl; 2D. Lateral view of the other flank.
Figure 3.	*Siberiptychites* (*Siberiptychites*) *stubendorffi* (Schmidt 1872). GSC 77096, GSC loc. 91310. Lateral view, x 1.
Figure 4.	*Siberiptychites* (*Pseudoeuryptychites*) *middendorffi* (Pavlow, 1914). GSC 77100, GSC loc. 91310. Juvenile whorls of the specimen reproduced in Pl. 34, fig. 3. Ventral view of the innermost whorl visible and cross-sections of the next two whorls, x 4. Note the absence of sculpture on the internal mould of the earliest visible whorl and the very wide and low, essentially *Euryptychites*-like cross-sections of the next two whorls (especially of the second whorl).


1C

1B

1A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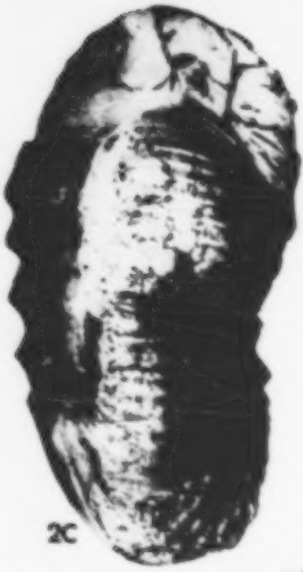
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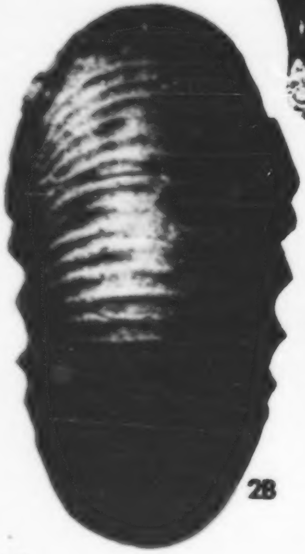
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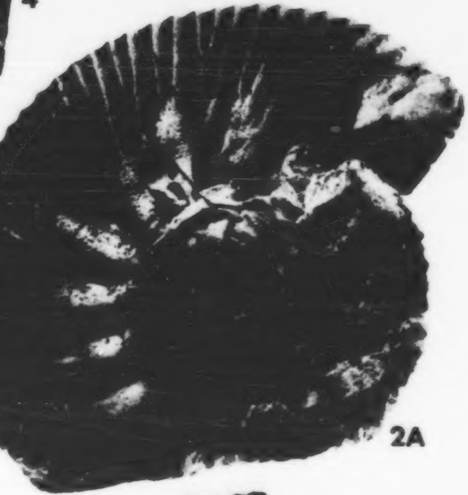
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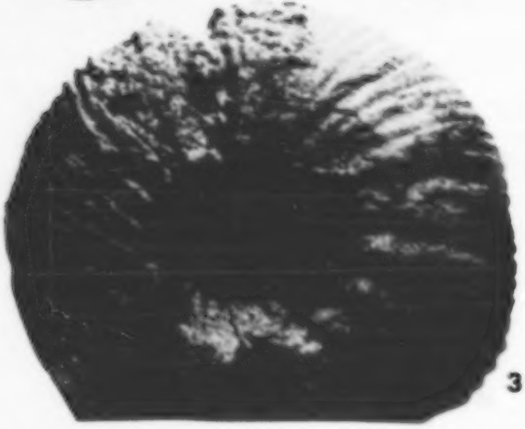
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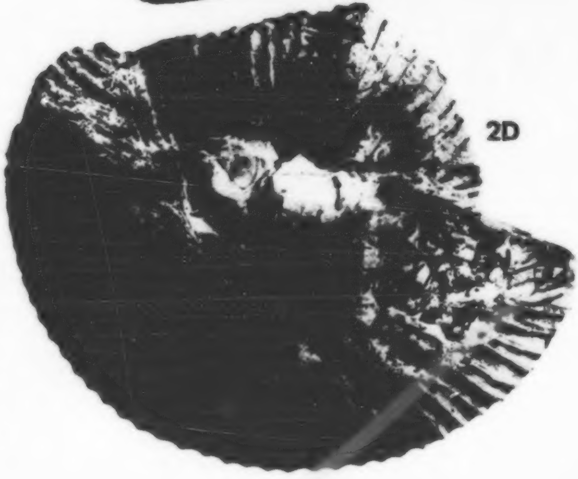

2D

Plate 33

Figure 1. *Polyptychites* aff. *P. tschekanovskii* Pavlow, 1914. GSC 77097, GSC loc. 82695. An entirely septate, considerably deformed phragmocone ending with ?penultimate whorl. Lateral view, x 1. See Pl. 35, figs. 1A-1C for other views of this specimen.

Figures 2A, 2B. *Siberiptychites* (*Siberiptychites*) n. sp. aff. *stubendorffi* (Schmidt, 1872). GSC 77098, GSC loc. 93754 (=GSC loc. 91308). Strongly deformed and fragmentary juvenile specimen, x 1. 1B. Lateral view of the inner whorl that exhibits well developed simple dichotomous sculptural stage followed by the earliest part of trivirgatitpartitous sculptural stage; 2A. Lateral view of the other flank that exhibits part of the next following whorl ornamented by typical trivirgatitpartitious bundles. Note the inked in external suture line.

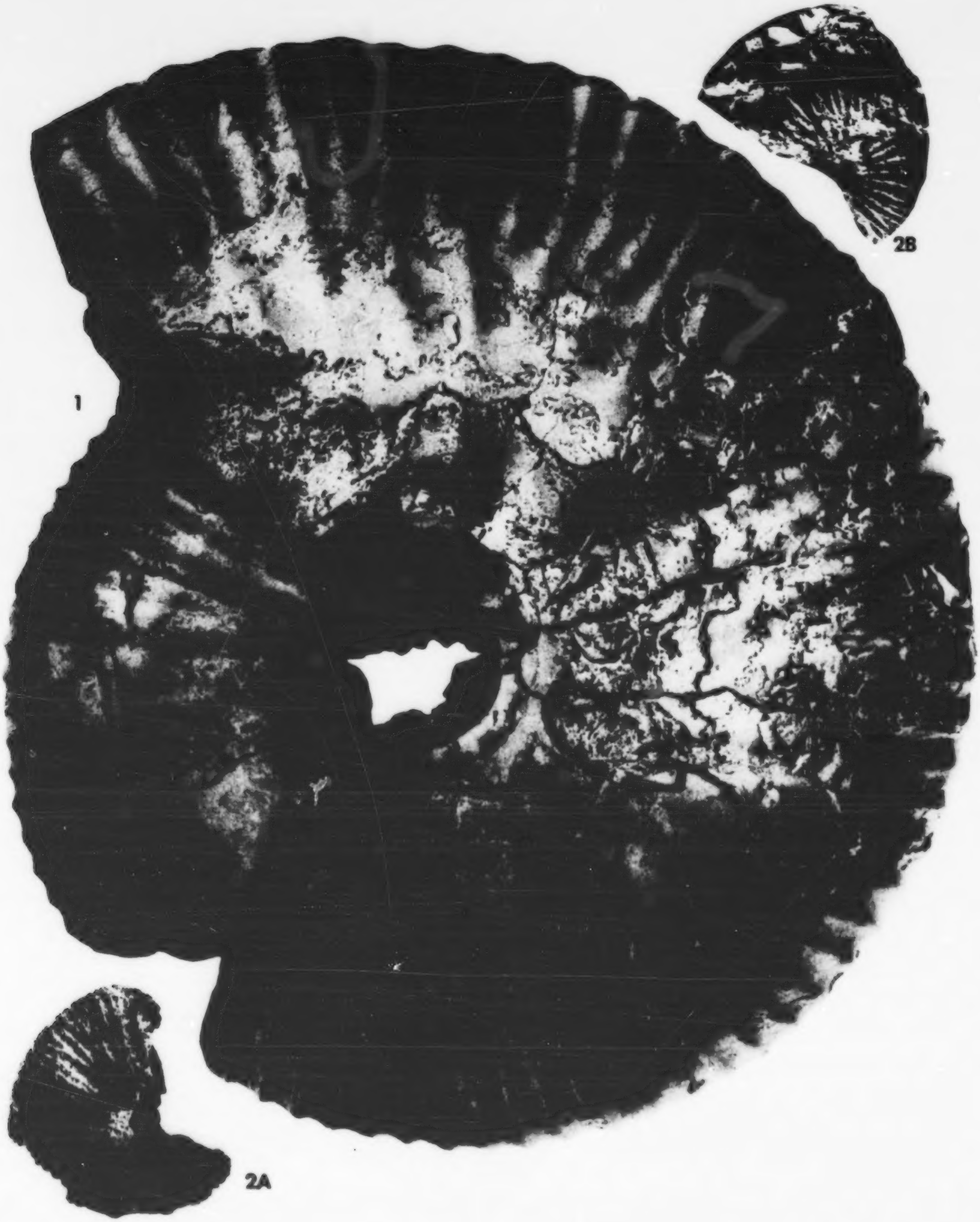

1
2A
2B

Plate 34

Figures 1A, 1B. *Polyptychites* aff. *P. tschekanovskii* Pavlow, 1914. GSC 77097. Cross-section and ventral view of the specimen reproduced in Pl. 33, fig. 1, x 1. 1A. Cross-sections of four intermediate and juvenile whorls and an imprint of the venter of preceding juvenile whorl. The outer three whorls are considerably deformed (laterally compressed). They may have been considerably wider and lower originally. If so, they were similar to equivalent whorls of *P. tschekanovskii* (compare Pl. 42, fig. 2; Pl. 67, fig. 1); 1B. Ventral view of the middle part of the last preserved whorl.

Figures 2A, 2B. *Siberiptychites* (*Pseudoeuryptychites*) *middendorffi* (Pavlow, 1914) GSC 77099, GSC loc. C-4749. Fragmentary and mostly deformed early and intermediate whorls, x 1. 2A. Lateral view; 2B. Ventral view of the almost underformed, last preserved part of the shell. See Pl. 40, figs. 2A, 2B for other views of this specimen.

Figures 3A-3E *Siberiptychites* (*Pseudoeuryptychites*) *middendorffi* (Pavlow, 1914). GSC 77100, GSC loc. 91310. All photographs, x 1. An excellently preserved, undeformed juvenile shell that is entirely septate. 3A. Lateral view; 3B. Lateral view of the other flank; 3C. Ventral view of the oral half of the whorl; 3D. Ventral view of its early third; 3E. Cross-section of the specimen with the ventral view of a segment of the earliest whorl (see Pl. 32, fig. 4 for its enlarged reproduction).

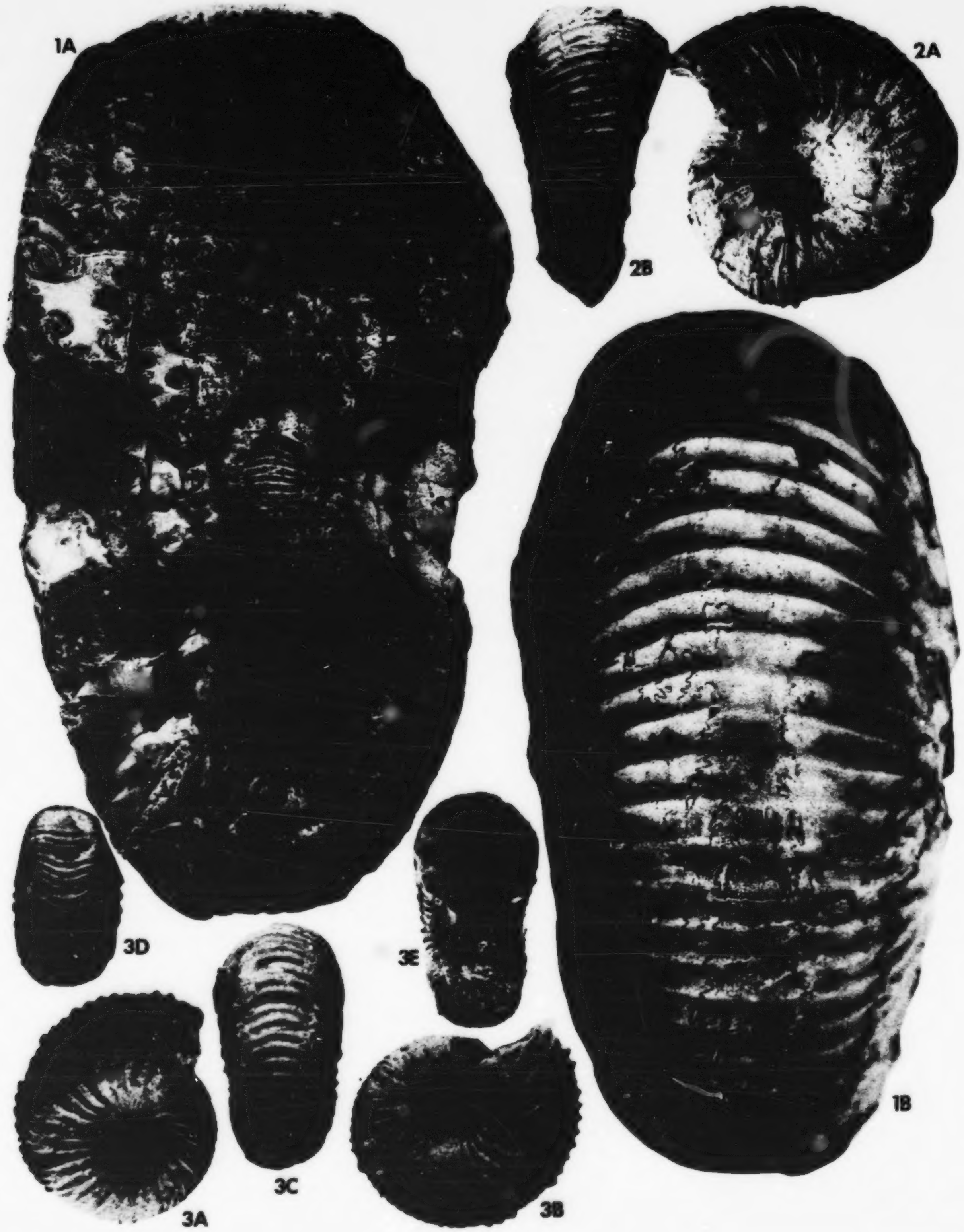
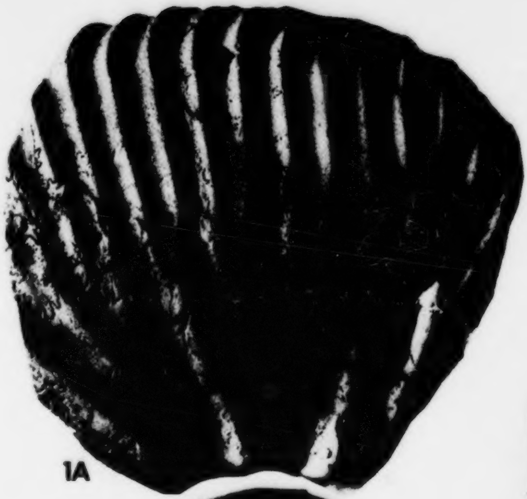
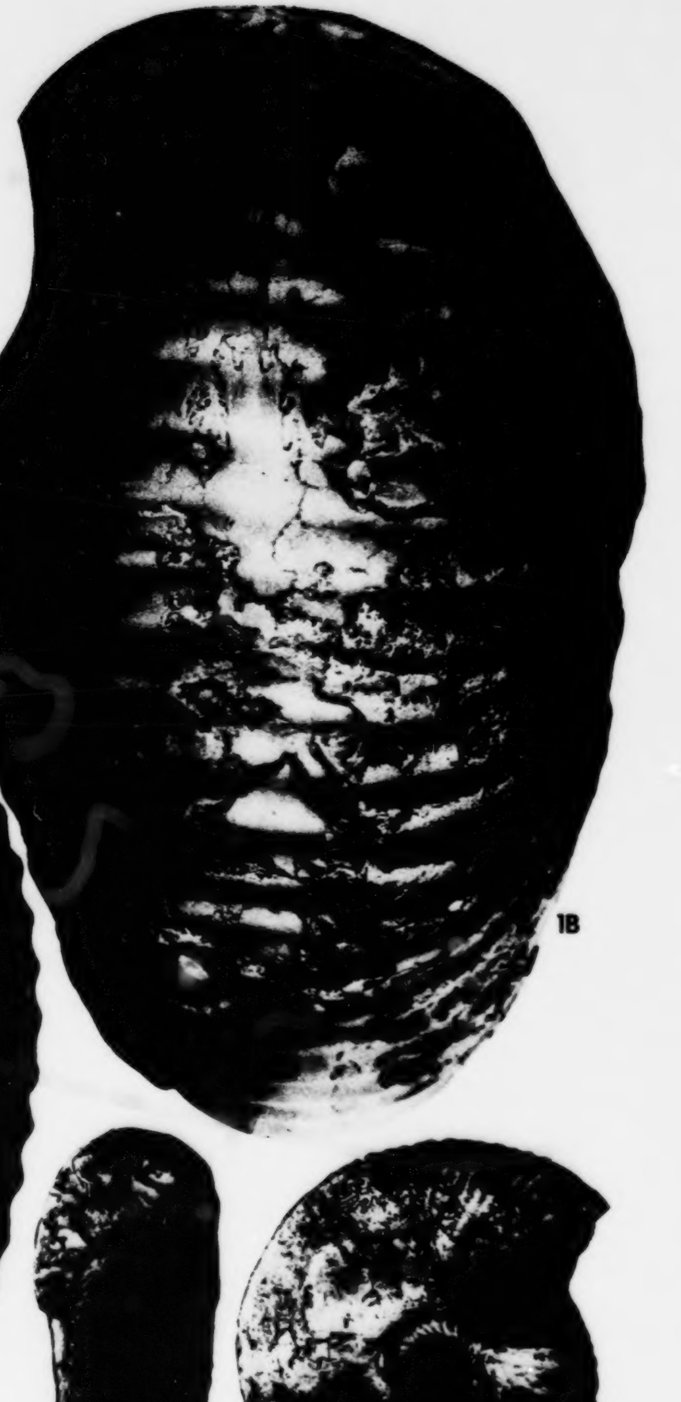

1A
2A
2B
1B
3D
3E
3C
3A
3B

Plate 35

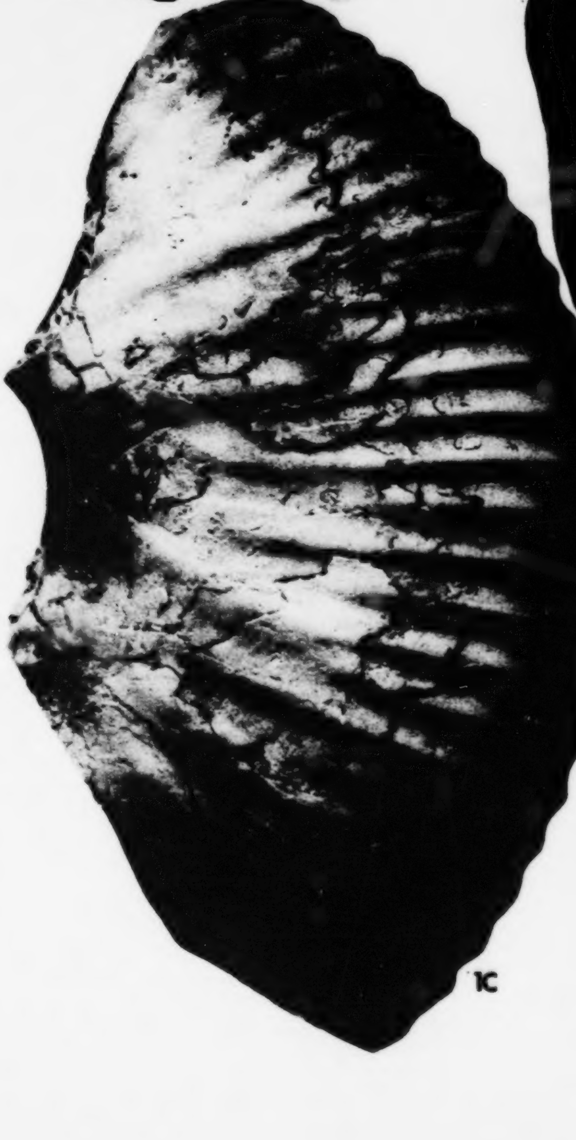
Figures 1A-1C.	*Polyptychites* aff. *P. tschekanovskii* Pavlow, 1914. GSC 77097, GSC loc. 82695. The same specimen as that reproduced in Pl. 33, fig. 1. All figures, x 1. 1A. Lateral view (somewhat oblique) of the earliest quarter-whorl of the flank reproduced in Pl. 33, fig. 1. Photographed in strong oblique light to elucidate details of bundling habit and external suture line; 1B. Ventral view of the oral one-half of the last preserved whorl; 1C. Lateral view of the middle part of the other flank where the sculpture begins to weaken in its middle.
Figures 2A, 2B.	*Siberiptychites* (*Siberiptychites*) *fascicostatus* n. sp. Holotype. GSC 17247, GSC loc. 37867. An entirely septate, somewhat deformed intermediate whorl, x 1. 2A. Lateral view; 2B. Oralmost preserved cross-section (deformed on the right flank) and ventral view of the early half of the whorl. See Pl. 39, fig. 2 for the ventral view of the oral half of the whorl.



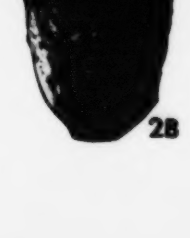
1A



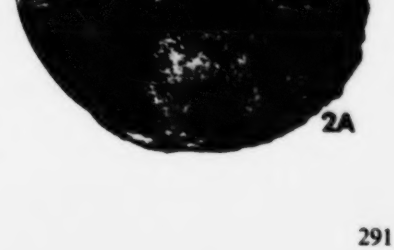
1B



1C



2B



2A

Plate 36

Figures 1A-1E.	*Siberiptychites (Siberiptychites) stubendorffi* (Schmidt, 1872). GSC 77101, GSC loc. 91310. Excellently preserved intermediate (?second penultimate) whorl of the slender variant. All photographs, x 1. 1A. Lateral view; 1B. Ventral view of the oral half of the whorl; 1C. Terminal cross-section and ventral view of the early half of the whorl; 1D. Obliquely lighted umbilicus showing the increased density and pinched appearance of primaries on the preceding whorls; 1E. Lateral part of external suture line near the oral end of the whorl.
Figures 2A, 2B.	*Siberiptychites (Pseudoeuryptychites) middendorffi* (Pavlow, 1914). GSC 77102, GSC loc. 91310. A completely septate, partly deformed, large specimen presumably representing the adult penultimate whorl, x 1. See Pl. 31, figs. 2A-2C for details of the external suture line dimly visible in Fig. 2A. 2A. Lateral view; 2B. Ventral view of the early half of the whorl that still retains the ribbing. Only the middle part of terminal cross-section is preserved.

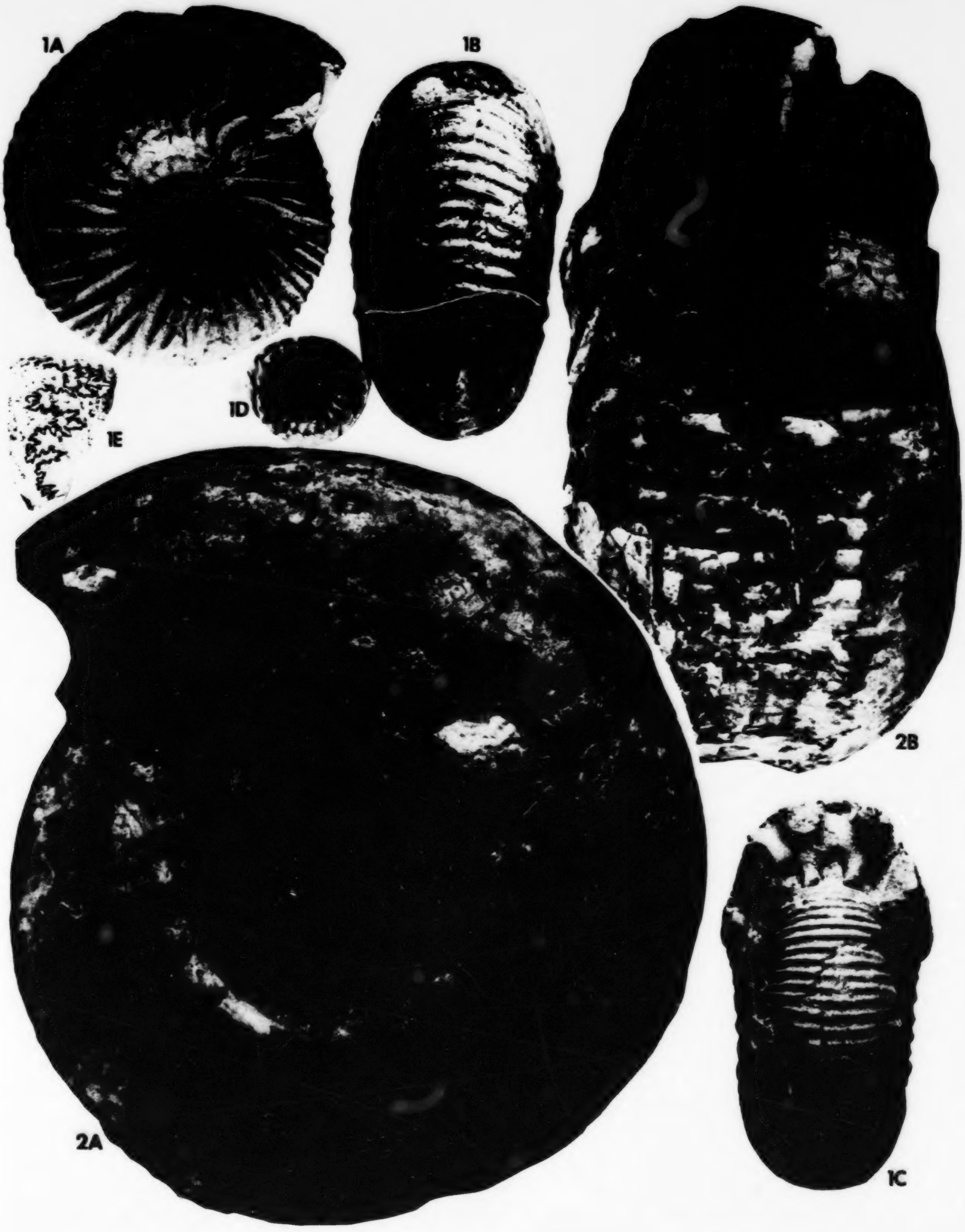

1A
1B
1E
1D
2B
2A
1C

Plate 37

Figures 1A-1B.	*Siberiptychites* (*Siberiptychites*) n. sp. aff. *stubendorffi* (Schmidt, 1872). GSC 77103, GSC loc. 91308. x 1. 1A. Lateral view; 1B. Ventral view.
Figures 2A-2C.	*Siberiptychites* (*Siberiptychites*) *stubendorffi* (Schmidt, 1872). GSC 77104, GSC loc. 91310. All figures x 1. 2A. Lateral view (photograph is trimmed); 2B. Lateral view of the other flank (untrimmed); 2C. Terminal cross-section and ventral view of the early half of the whorl.
Figures 3A, 3B.	*Siberiptychites* (subgenus novum)? sp. nov. B. GSC 77105, GSC loc. 91310. A fragmentary, presumably adult specimen, the last preserved whorl fragment of which is an ?adult living chamber. 3A. Lateral view; 3B. Ventral view.

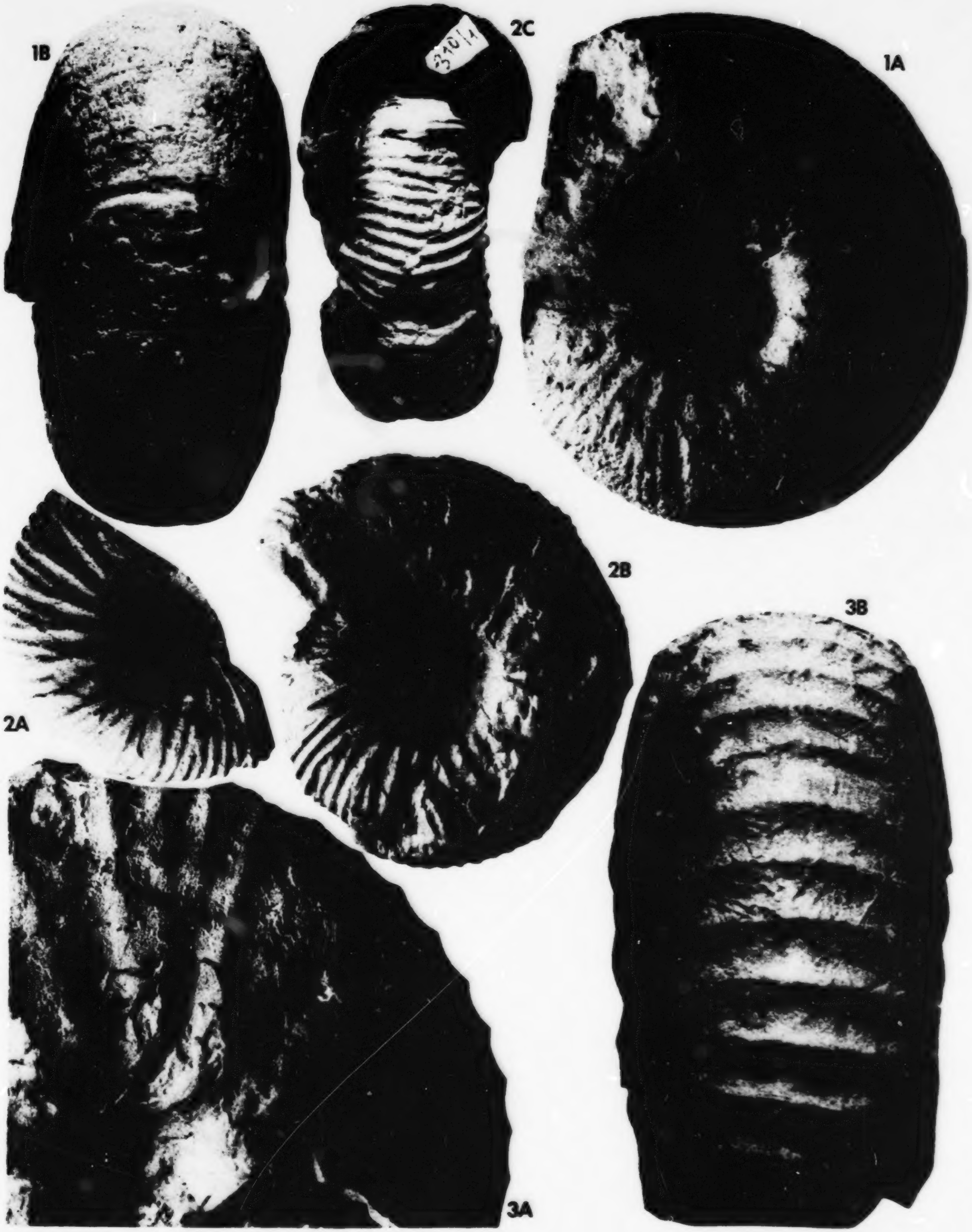

1B
2C
3101/1
1A
2B
3B
2A
3A

Plate 38

Figures 1A-1F. *Siberiptychites* n. sp. aff. *stubendorffi* (Schmidt, 1872). GSC 77106, GSC loc. 82695. This entirely septate specimen consists of fragments of seven juvenile to advanced intermediate whorls beginning with the second earliest whorl and ending with ?second penultimate whorl. 1A. Lateral view, x 1; 1B. Terminal cross-section of the last preserved whorl and ventral view of the preceding whorl, x 1; 1C. Lateral view of a segment of the fourth from the last whorl (it is visible on the left side of fig. 1A) ornamented by simple dichotomous rib bundles, x 2; 1D. Lateral view of the other flank of this fragment ornamented by intercalated simple dichotomous and trivirgatitpartitous rib bundles, x 2; 1E. Ventral view of the same fragment, x 2; 1F. Cross-section of the same fragment, venter above, x 2. See Pl. 42, fig. 1 for the cross-section of this specimen.

Figures 2A-2B. *Siberiptychites* (*Pseudoeuryptychites*) *pateraeformis* (Voronets, 1962). GSC 77107, GSC loc. 91309. Strongly deformed, large but entirely septate representative of the species, x 1. 2A. Lateral view; 2B. Terminal cross-section and ventral view of the early part of the last preserved whorl. Note the straight umbilical wall and angular umbilical shoulder on the right flank of the cross-section that are characteristic of the subgenus *Pseudoeuryptychites*.

Figures 3A, 3B. *Siberiptychites* (*Siberiptychites*) *stubendorffi* (Schmidt, 1872). GSC 77108, GSC loc. 91311. A fairly strongly deformed, large representative of the intermediate variant. This entirely septate specimen appears to include most of the adult penultimate whorl. 3A. Lateral view of last preserved whorl with the displaced early juvenile whorl visible inside the umbilicus, x 1; 3B. Lateral view of this early juvenile whorl, x 3. The early two-thirds of the whorl only bear some striae and constrictions (the essentially smooth sculptural stage) while its oral one-third is ornamented by single to bifurcating ribs (the beginning of the *Bodylevskites*-like sculptural stage).

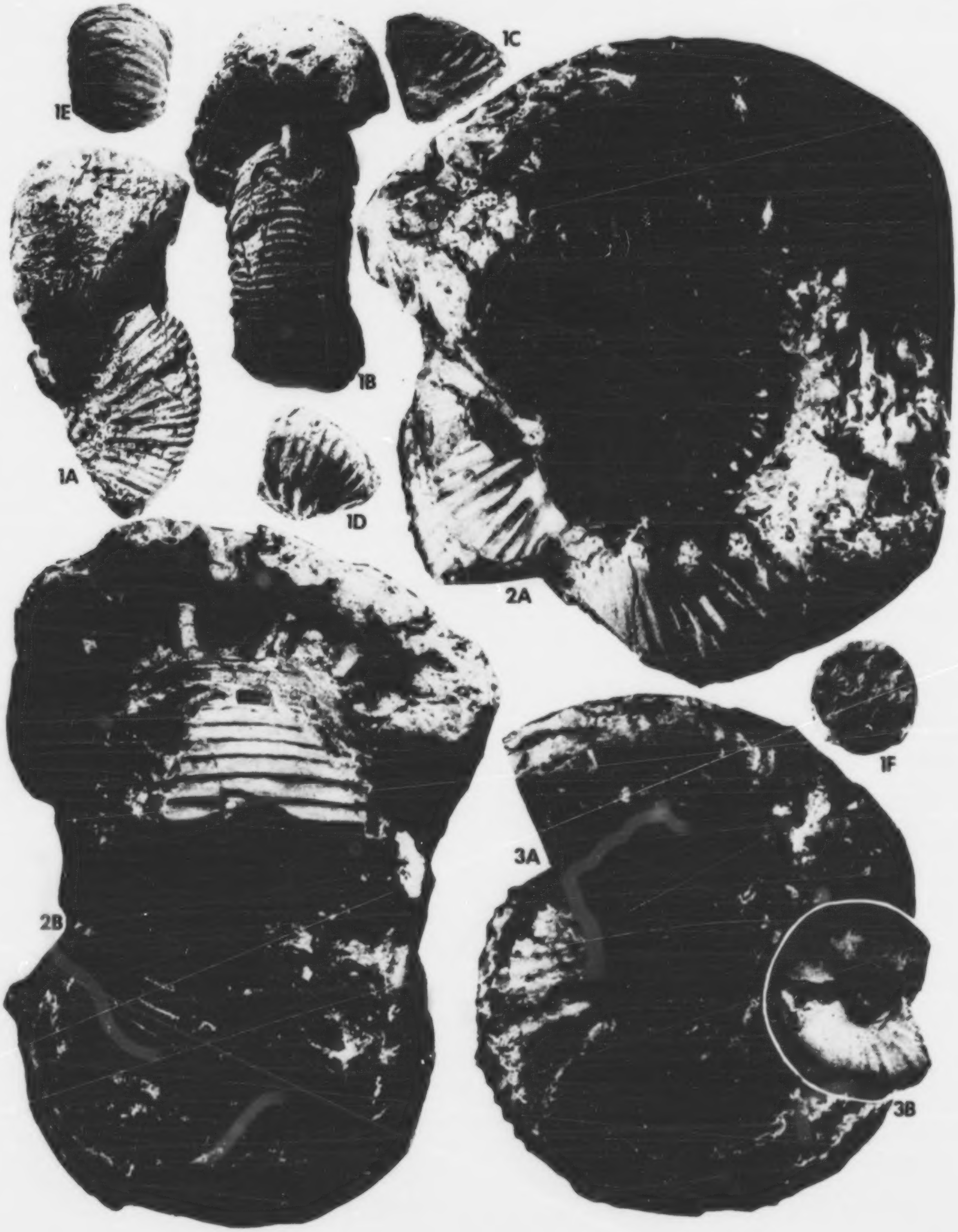
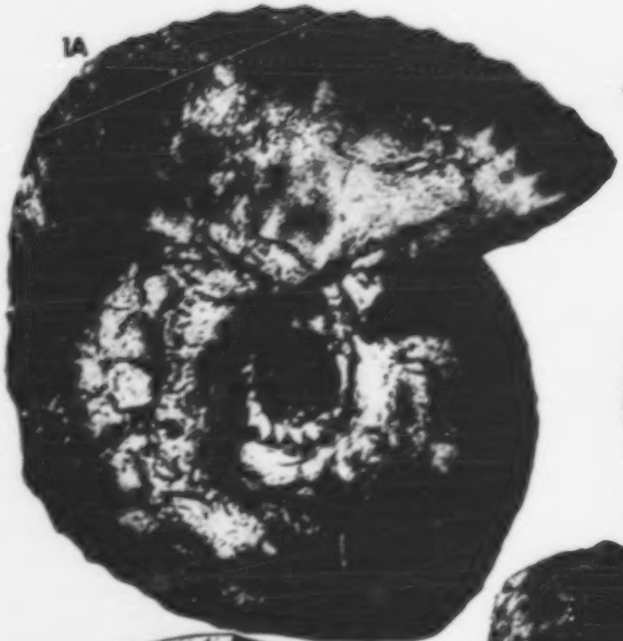

1E
1C
1B
1A
1D
2A
1F
3A
2B
3B

Plate 39

Figures 1A-1C.	*Siberiptychites* (*Siberiptychites*) *stubendorffi* (Schmidt, 1872). GSC 17244, GSC loc. 37867. A partly deformed adult representative of the sturdy variant retaining the early part (about one-quarter whorl) of the living chamber, x 1. 1A. Lateral view; 1B. Lateral view of the other flank with ribs and bullae outlined in black; 1C. Essentially undeformed terminal cross-section and ventral view of the undeformed early third of the penultimate whorl.
Figure 2.	*Siberiptychites* (*Siberiptychites*) *fascicostatus* n. sp. Holotype. GSC 17247, GSC loc. 37867. Ventral view of the specimen reproduced in Pl. 35, fig. 2, x 1.
Figures 3A-3H	*Siberiptychites* (*Pseudoeuryptychites*) *middendorffi* (Pavlow, 1914) var. *incrassata* (Pavlow, 1914). GSC 17251, GSC loc. 37867. Fragments of early to intermediate whorls of a typical representative of the variant. The last preserved whorl (Fig. 3A) includes what appears to be the very beginning of intermediate living chamber. All photographs, except for 3G, 3F and 3H, are, x 1. 3A. Lateral view of last preserved whorl; 3B. Ventral view of the same; 3C. Cross-section of the last preserved whorl and that of the preceding whorl; 3D. Terminal cross-section and ventral view of a rubber mould of the fragment of the third from the last whorl that is only preserved as an impression (see Fig. 3C); 3E. Lateral view of the same rubber mould. The umbilical shoulder and the lower flank are not preserved. The coarse, widely spaced and prominent secondary ribs contrast with fine, closely spaced low secondaries of the preceding juvenile whorl (see Figs. 3F, 3G); 3F. Lateral view of a fragment of the fourth whorl before last. The fine and closely spaced trivirgatitpartitous rib bundles of the early part of the fragment are *Astieriptychites*- or *Bodylevskites*-like. They rapidly become coarser, more widely spaced and more prominent on its oral part, x 2; 3G. Ventral view of the same fragment, x 2; 3H. Cross-section of the same fragment, x 2. Note its essentially *Euryptychites*-like shape and proportions.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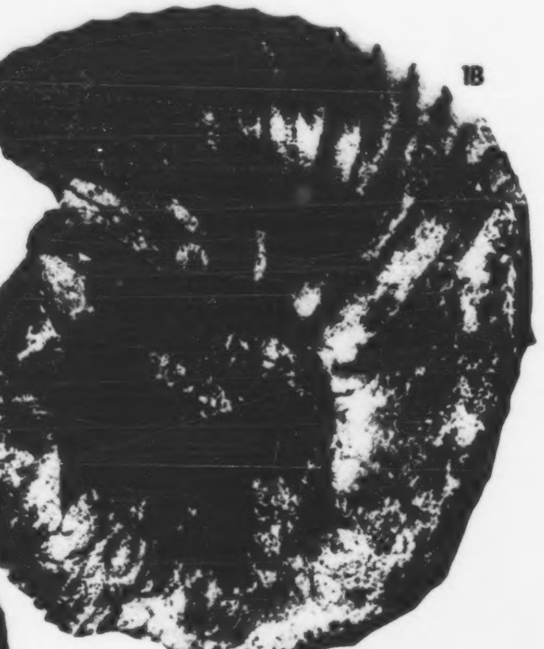
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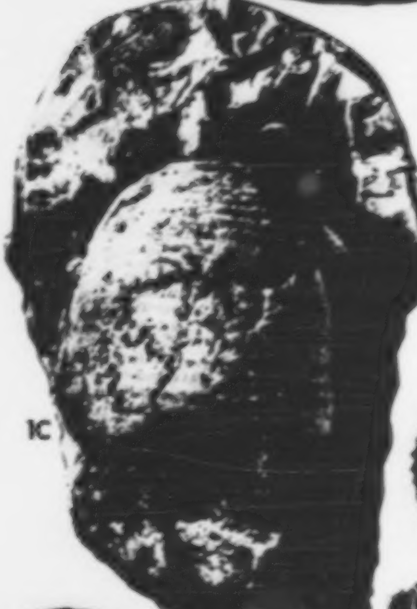
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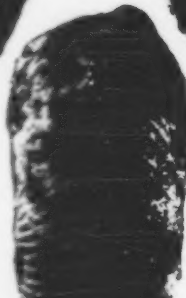
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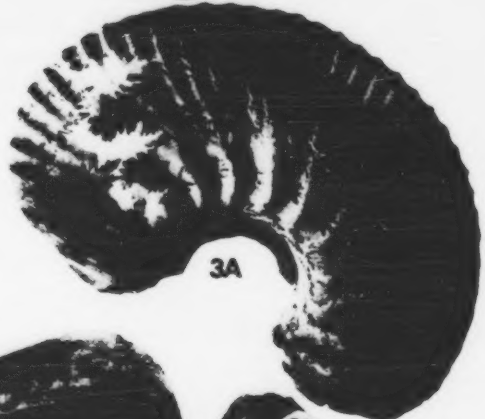
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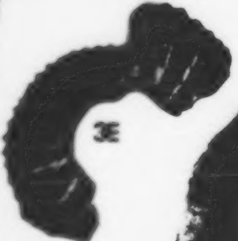
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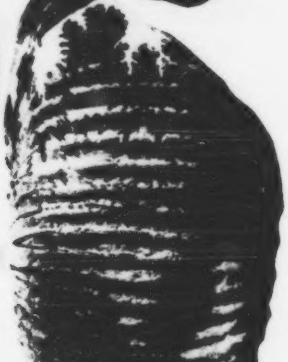
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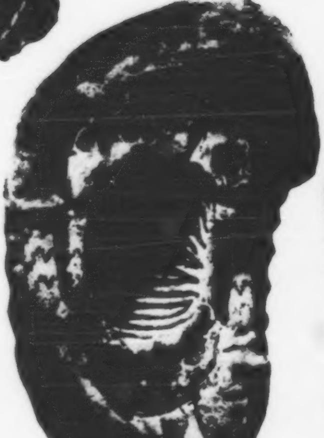
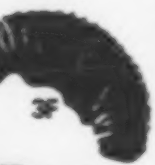

3C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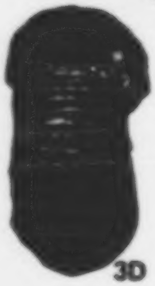
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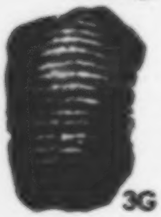

3G

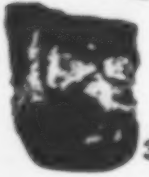

3H

Plate 40

Figure 1	*Polyptychites tschekanovskii* Pavlow, 1914. GSC 77109, GSC loc. 91302. Lateral view of the oral part of second penultimate and early part of first penultimate whorl of the apparently adult specimen, x 1. See Pl. 41, fig. 1 and Pl. 42, fig. 2 for the reproduction of the anterior part of its penultimate whorl and fragmentary early part of its ultimate whorl (a living chamber).
Figures 2A-2B	*Siberiptychites* (*Pseudoeuryptychites*) *middendorffi* (Pavlow, 1914). GSC 77099, GSC loc. C-4749. Ventral view (Fig. 2A) and cross-section (Fig. 2B) of the specimen reproduced in Pl. 34, fig. 2. Both photographs, x 1.
Figures 3A-3F.	*Siberiptychites* (*Pseudoeuryptychites*) *middendorffi* (Pavlow, 1914). var. *incrassata* (Pavlow, 1914). GSC 17251, GSC loc. 37867. Rubber mould of a partial imprint (lacks the umbilical shoulders and lower flanks) of the ?third or ?fourth juvenile whorl preserved inside the innermost bodily preserved whorl of the specimen reproduced in Pl. 39, fig. 3H. This imprint (an internal mould) represents the initial or globular growth stage of the whorl shape and proportions of *S.* (*P.*) *middendorffi* and its smooth sculptural growth stage. 3A. Lateral view, x 1; 3B. Ventral view, x 1; 3C. Lateral view of the other flank, x 1; 3D. The same view as in 3C but x 4 to elucidate its structural detail; 3E. The same view as in 3A but x 4 to elucidate its structural details; 3F. The same view as in 3B but x 4 to elucidate its structural details. Note the well preserved suture line.

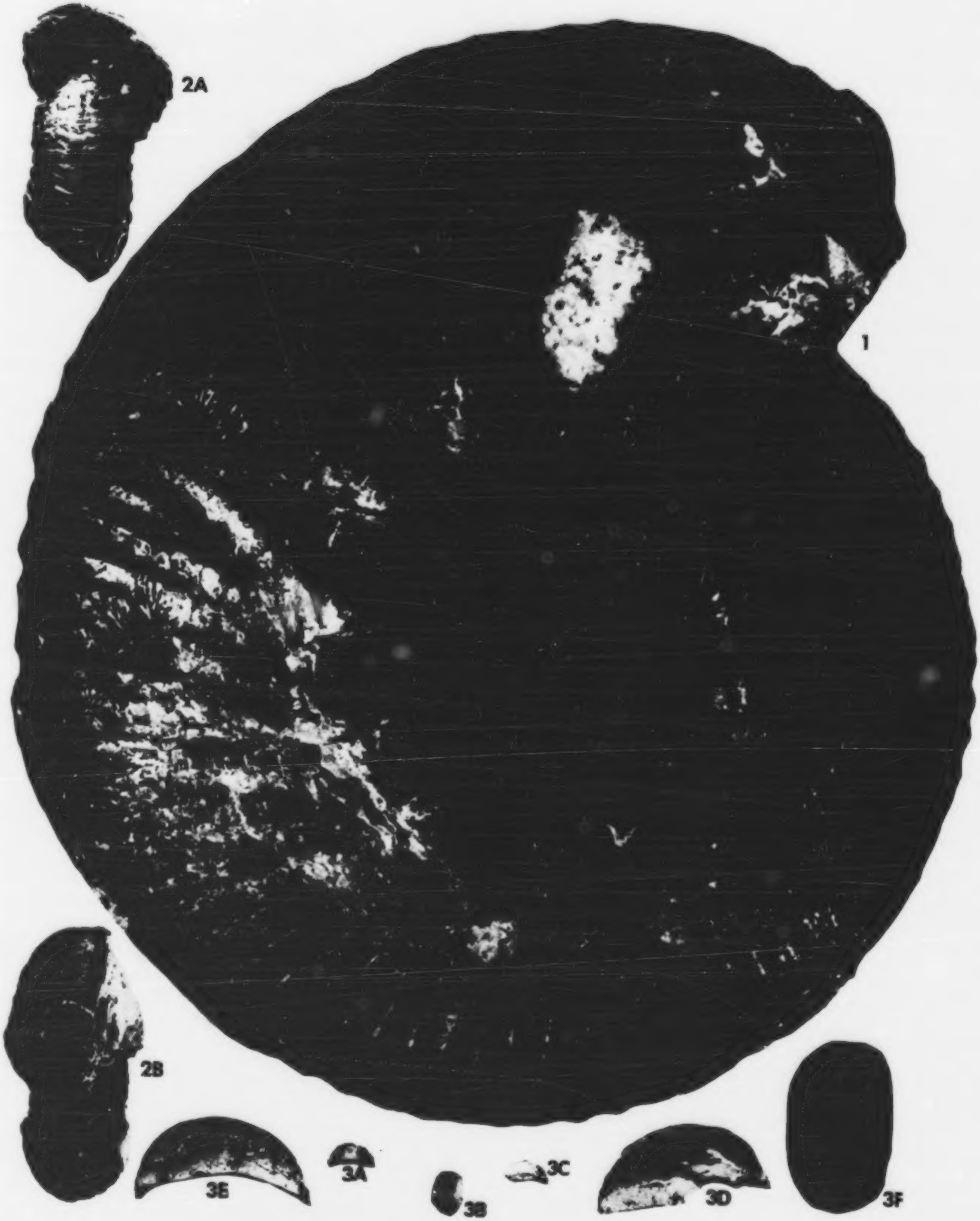

2A
1
2B
3E
3A
3B
3C
3D
3F

Plate 41

Figure 1. *Polyptychites tschekanovskii* Pavlow, 1914. GSC 77109, GSC loc. 91302. Lateral view of the oral part of penultimate whorl and the fragmentary early part of ultimate whorl of the specimen reproduced in Pl. 40, fig. 1, x 0.9.

1

Plate 42

Figure 1.	*Siberiptychites* (*Siberiptychites*) n. sp. aff. *stubendorffi* (Schmidt, 1872). GSC 77106. Cross-section of the specimen reproduced in Pl. 38, fig. 1, x 1. See there for further details.
Figure 2.	*Polyptychites tschekanovskii* Pavlow, 1914. GSC 77109, GSC loc. 91302. Specimen reproduced in Pl. 40, fig. 1 and Pl. 41, fig. 1. Partly preserved and deformed terminal cross-section and the ventral view of oral part of penultimate whorl, x 1.
Figure 3.	*Astieriptychites obsoletus* n. sp. Holotype, GSC 77110, GSC loc. 93865. Lateral view with the last preserved one-half whorl taken off, x 1. See Pl. 49, fig. 2; Pl. 57, fig. 4; Pl. 59, fig. 4 and Pl. 62, fig. 2 for other photographs of this specimen.
Figure 4.	*Siberiptychites* (*Siberiptychites*) *stubendorffi* (Schmidt, 1872). GSC 77111, GSC loc. 91354. Lateral view of intermediate whorl, x 1. This whorl displays simple dichotomous rib bundles on its earliest one-quarter and trivirgatitpartitous rib bundes on its oral half. See Pl. 43, fig. 3, Pl. 44, fig. 2, and Pl. 64, fig. 2 for other views of this specimen.
Figures 5A, 5B.	*Astieriptychites*? sp. indet. B. GSC 77112, GSC loc. 91376. 5A. Lateral view of an almost completely flattened intermediate whorl, x 1; 5B. Lateral view of the other flank of the same whorl, x 1.

1

3

4

2

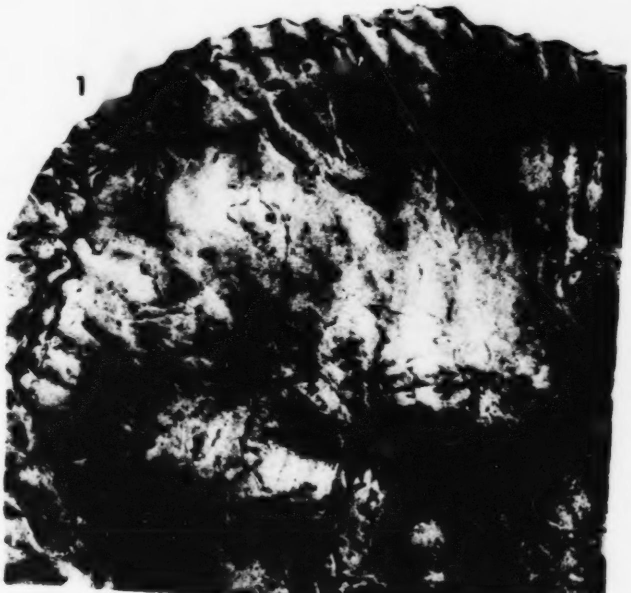
5A

5B

Plate 43

Figure 1	*Polyptychites canadensis* Kemper and Jeletzky, 1979. Paratype. GSC 77113, GSC loc. 85025. Lateral view of a segment of inner whorl visible in the last preserved whorl of the large specimen reproduced in Pl. 46, fig. 2; Pl. 48, fig. 2 and Pl. 65, fig. 1, x 1.
Figures 2A-2C.	*Polyptychites* aff. *P. hapkei* n. sp. GSC 77114, GSC loc. 82695. 2A. Ventral view; 2B. Lateral view; 2C. Cross-section. All photographs, x 1.
Figure 3	*Siberiptychites* (*Siberiptychites*) *stubendorffi* (Schmidt 1872). GSC 77111. Lateral view of the specimen reproduced in Pl. 42, fig. 4, x 1. See there for further details.

1



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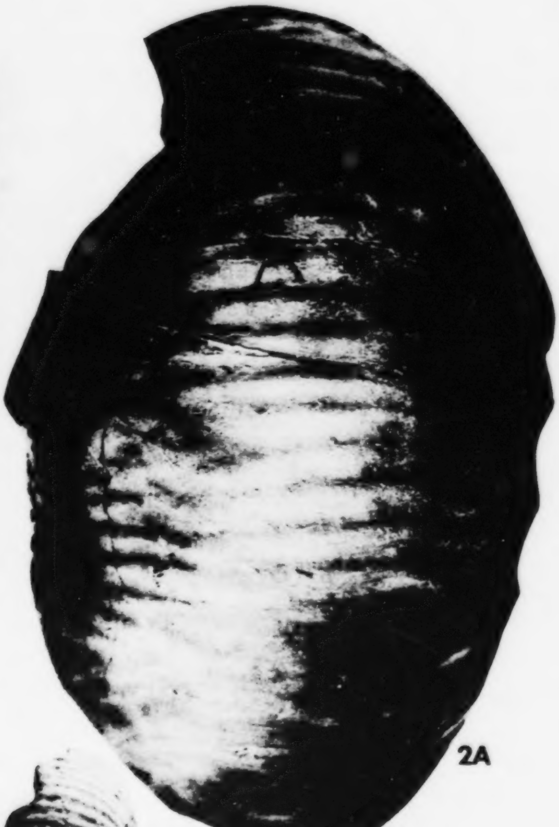

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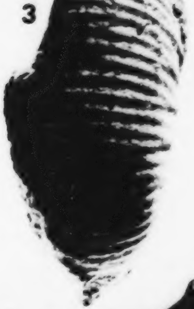
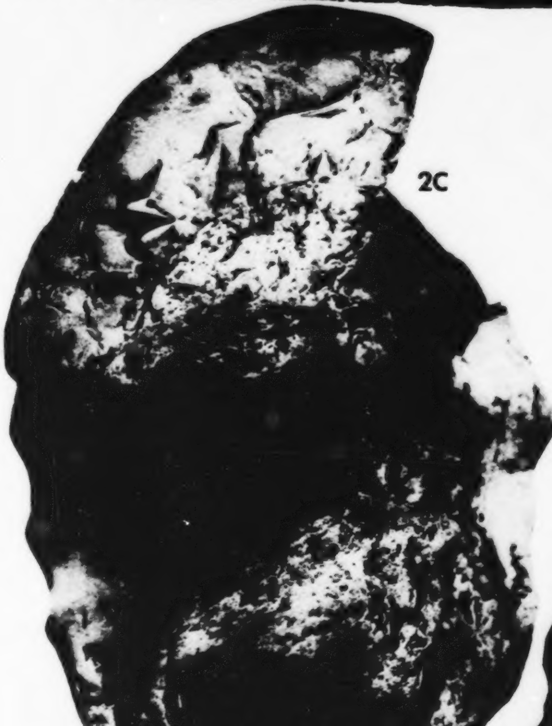


2C



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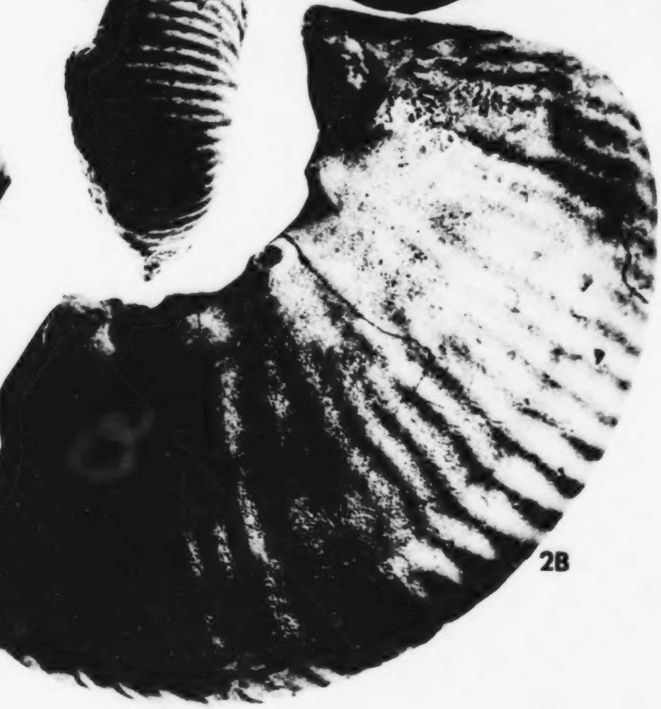
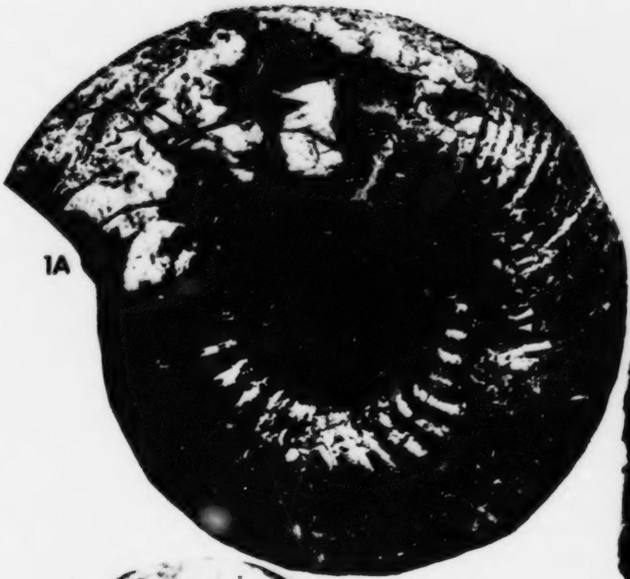


Plate 44

Figures 1A, 1B.	*Siberiptychites* (*Siberiptychites*) *stubendorffi* (Schmidt, 1872). GSC 77115, GSC loc. 91310. Partly deformed, large representative of the sturdy variant. This fully septate whorl appears to be largely or ?entirely adult penultimate whorl, x 1. 1A. Lateral view; 1B. Ventral view.
Figures 2A-2B.	*Siberiptychites* (*Siberiptychites*) *stubendorffi* (Schmidt, 1872). GSC 77111, GSC loc. 91354. The specimen reproduced in Pl. 42, fig. 4, and Pl. 43, fig. 3 with the last one-half whorl removed to expose the predominantly simple dichotomous ornamentation of preceding half whorl. Note well developed constriction on its innermost exposed part, x 1. 2A. Lateral view; 2B. Ventral view of the earliest exposed half-whorl.
Figure 3	*Siberiptychites* (*Siberiptychites*) *stubendorffi* (Schmidt, 1872). GSC 77116, GSC loc. 91310. Adult representative of the intermediate variant morphologically transitional to the sturdy variant. The specimen includes about one-half whorl of adult living chamber. Note a large pathological swelling in the whorl's middle that causes a strong disorganization of the ribbing habit. Lateral view, x 1.
Figure 4.	*Polyptychites balkwilli* n. sp. Holotype. GSC 77117, GSC loc. 91302. This largest known representative of the species is septate to its preserved oral end and must have extended for at least one more whorl. Ventral view of the best preserved middle part of the whorl, x 1. See Pl. 45, fig. 1 for the lateral view.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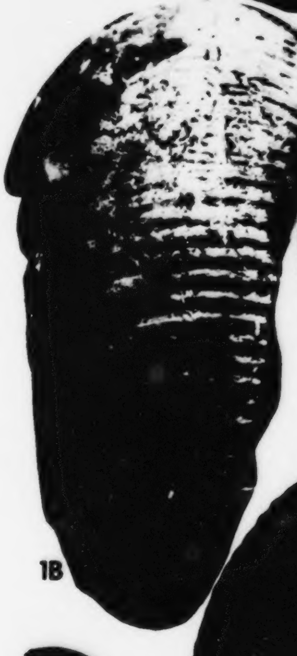
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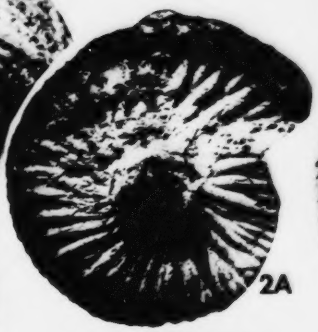
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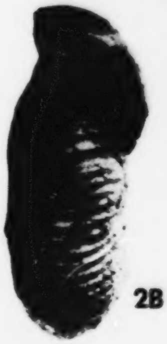
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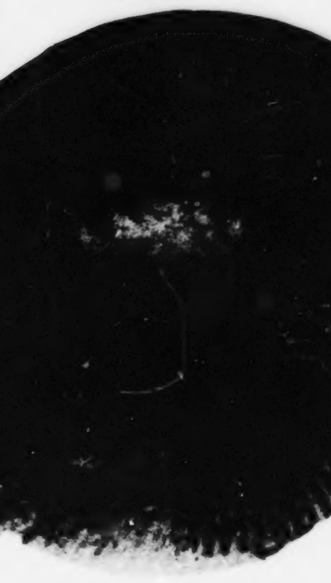
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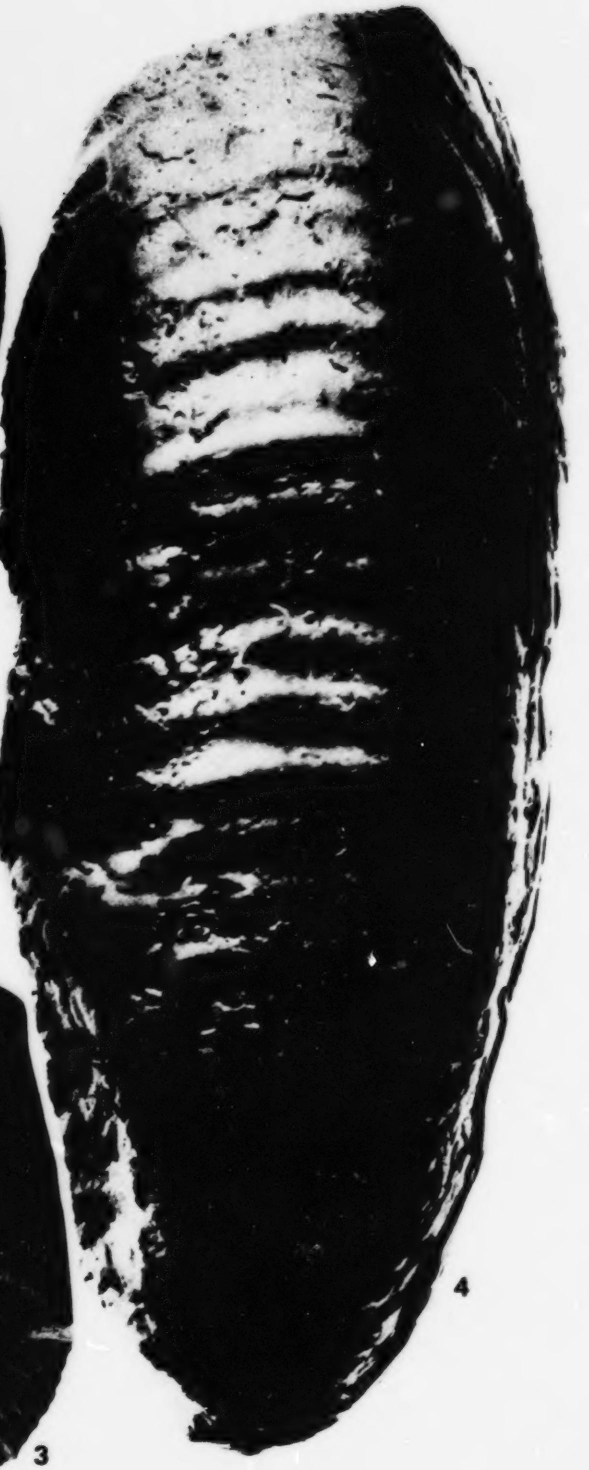
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Plate 45

Figure 1. *Polyptychites balkwilli* n. sp. Holotype. 77117, GSC loc. 91302. Lateral view of the better preserved flank of the specimen reproduced in Pl. 44, fig. 4, x 1. Note the almost complete obliteration of primary and secondary ribs on the flank of the oral half of this fully septate whorl, which contrasts with the simultaneously increasing prominence of umbilical nodes and the retention of secondary ribs on the ventral shoulder and venter proper (compare Pl. 44, fig. 4).

Figure 2. *Prodichotomites* aff. *P. hollwedensis* Kemper, 1978. GSC 77118, GSC. loc. 85023. A non-whitened oblique lateral view of well exposed external suture line on the earliest exposed part of the penultimate whorl (compare Pl. 49, fig. 3B that is whitened to show the bundling habit), x 1. The auxiliary part of the suture consists of three lobes, of which only the third auxiliary is situated on the umbilical wall (compare Figure 50), x 2.

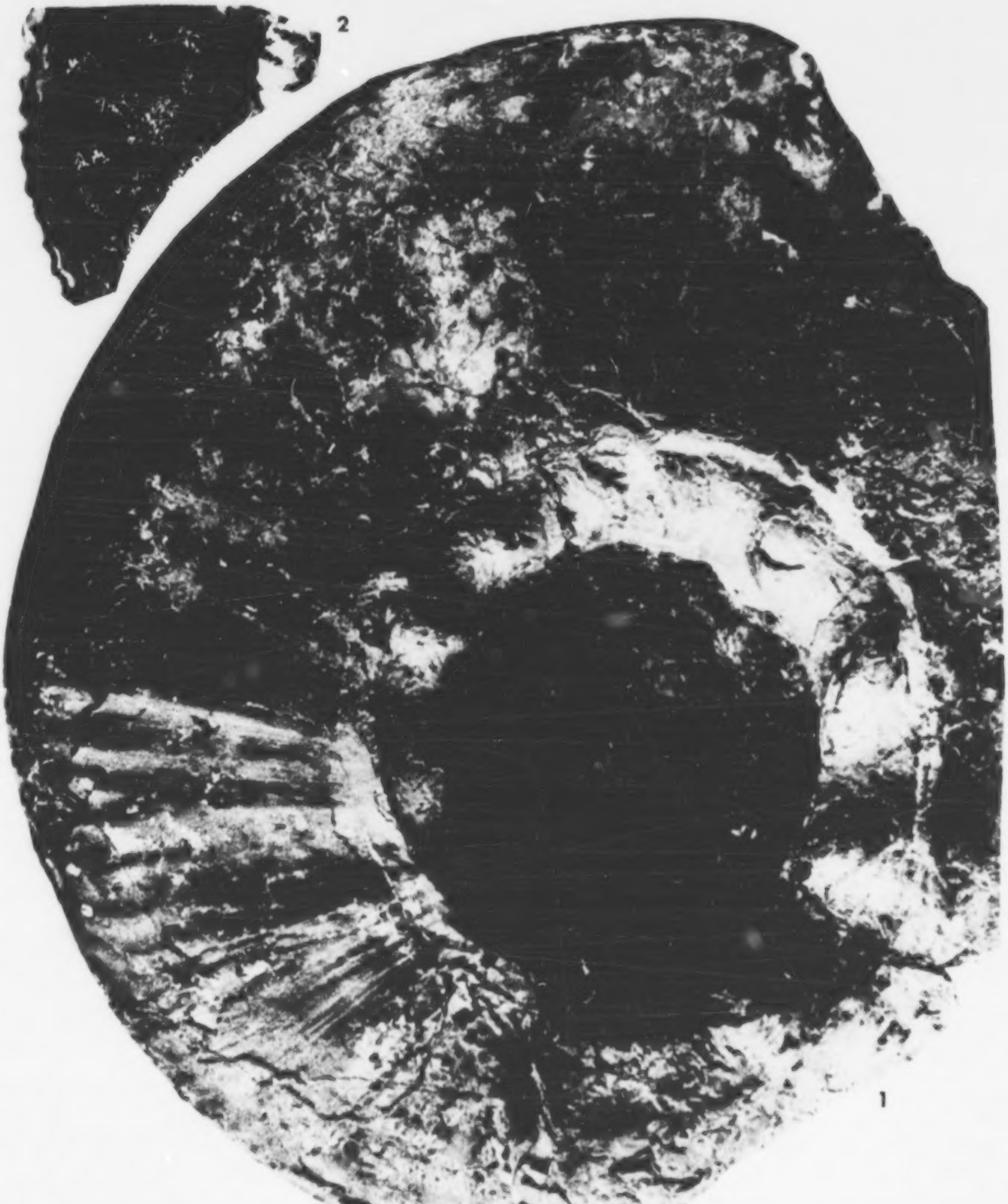

2
1

Plate 46

Figure 1. *Siberiptychites* (*Pseudoeuryptychites*) sp. indet. A. GSC 77119, GSC loc. 93754 (= 91308). Fragment of the inner whorl of the specimen shown in Pl. 67, fig. 2. The cross-section of this fragment is visible there in Fig. 2B while a part of its coarsely ribbed venter is indicated by an arrow in fig. 2A. An oblique lateral view, x 1.

Figure 2. *Polyptychites canadensis* Kemper and Jeletzky, 1979. Paratype. GSC 77113, GSC loc. 85025. Lateral view of the complete specimen, x 0.5. The fragmentary last preserved whorl of this largest known representative of *P. canadensis* includes the beginning of the living chamber. Therefore, it is believed to include all of the adult penultimate whorl.

Figure 3. *Prodichotomites* aff. *P. hollwedensis* Kemper, 1878. GSC 77118, GSC loc. 85023. Another view of the external suture lines shown in Pl. 45, fig. 2 oriented so as to bring their first and second lateral lobes into the foreground, x 2. Note the asymmetrically bifid termination of the first lateral lobe.

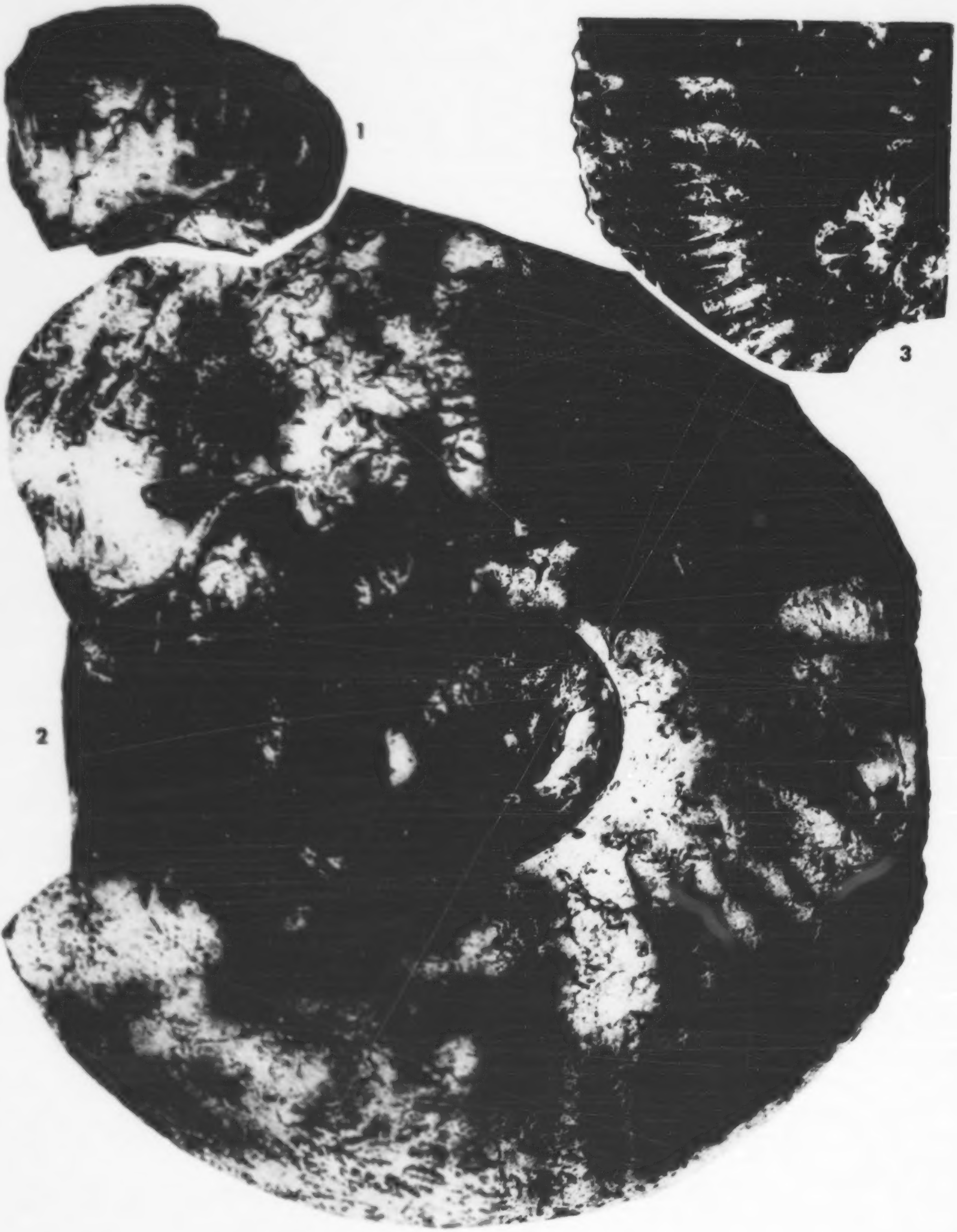

1
2
3

Plate 47

Figures 1A-1D.	*Amundiptychites* aff. *sverdrupi* Kemper and Jeletzky, 1979. GSC 61762, GSC loc. 85059. Fragmentary intermediate and early whorls of a form closely allied to *A. sverdrupi* and possibly representing its extreme morphological variant. All photographs x 1. 1A. Lateral view; 1B. Lateral view of the other flank; 1C. Ventral view of the oralmost preserved whorl; 1D. Cross-sections of five intermediate and early whorls.
Figure 2.	*Polyptychites canadensis* Kemper and Jeletzky, 1979. Paratype. GSC 77113, GSC loc. 85025. Ventral view of the middle, undeformed third of the oralmost preserved whorl of the specimen reproduced in Pl. 46, fig. 2, x 1.

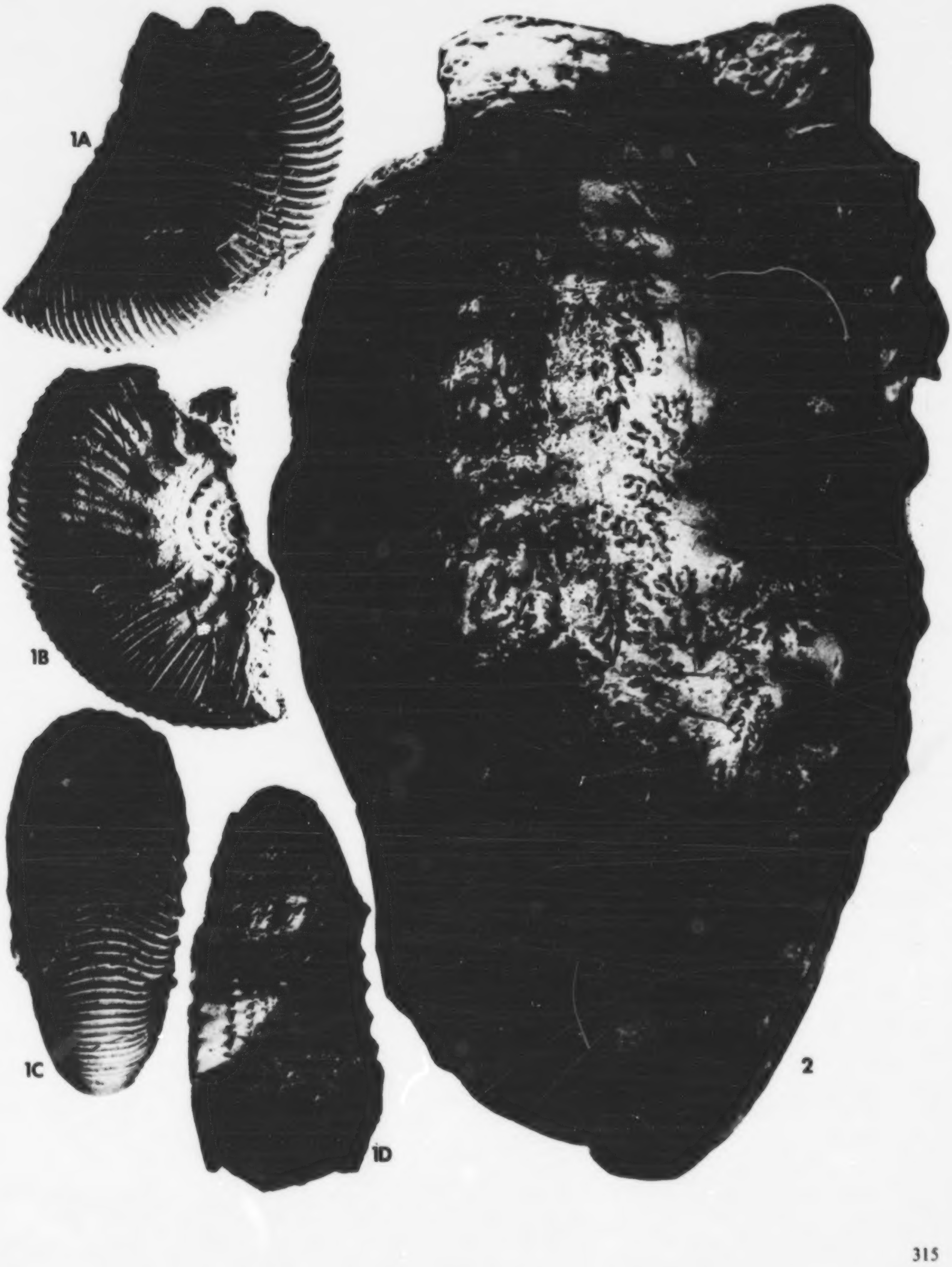

1A
1B
1C
1D
2

Plate 48

Figures 1A-1B. *Amundiptychites sverdrupi* Kemper and Jeletzky, 1979. First paratype. GSC 61765, GSC loc. 91303. A late early whorl and an intermediate whorl (compare Pl. 49, figs. 1A, 1B) followed by a fragment of an intermediate living chamber, x 1. 1A. Lateral view of penultimate preserved whorl. 1B. Ventral view of penultimate preserved whorl and the fragmentary left lower flank of the ultimate preserved whorl. Note huge conical umbilical nodes of the latter.

Figure 2. *Polyptychites canadensis* Kemper and Jeletzky, 1979. Paratype. GSC 77113, GSC loc. 85025. Ventral view of the early deformed part of the last preserved whorl of the specimen reproduced in Pl. 43, fig. 1 and Pl. 46, fig. 2, x 1. Part of the last whorl is taken off to show the characteristically prominent ribbing on the venter of the preceding whorl. See Pl. 43, fig. 1 and Pl. 65, fig. 1 for the lateral views of that segment of the preceding whorl.

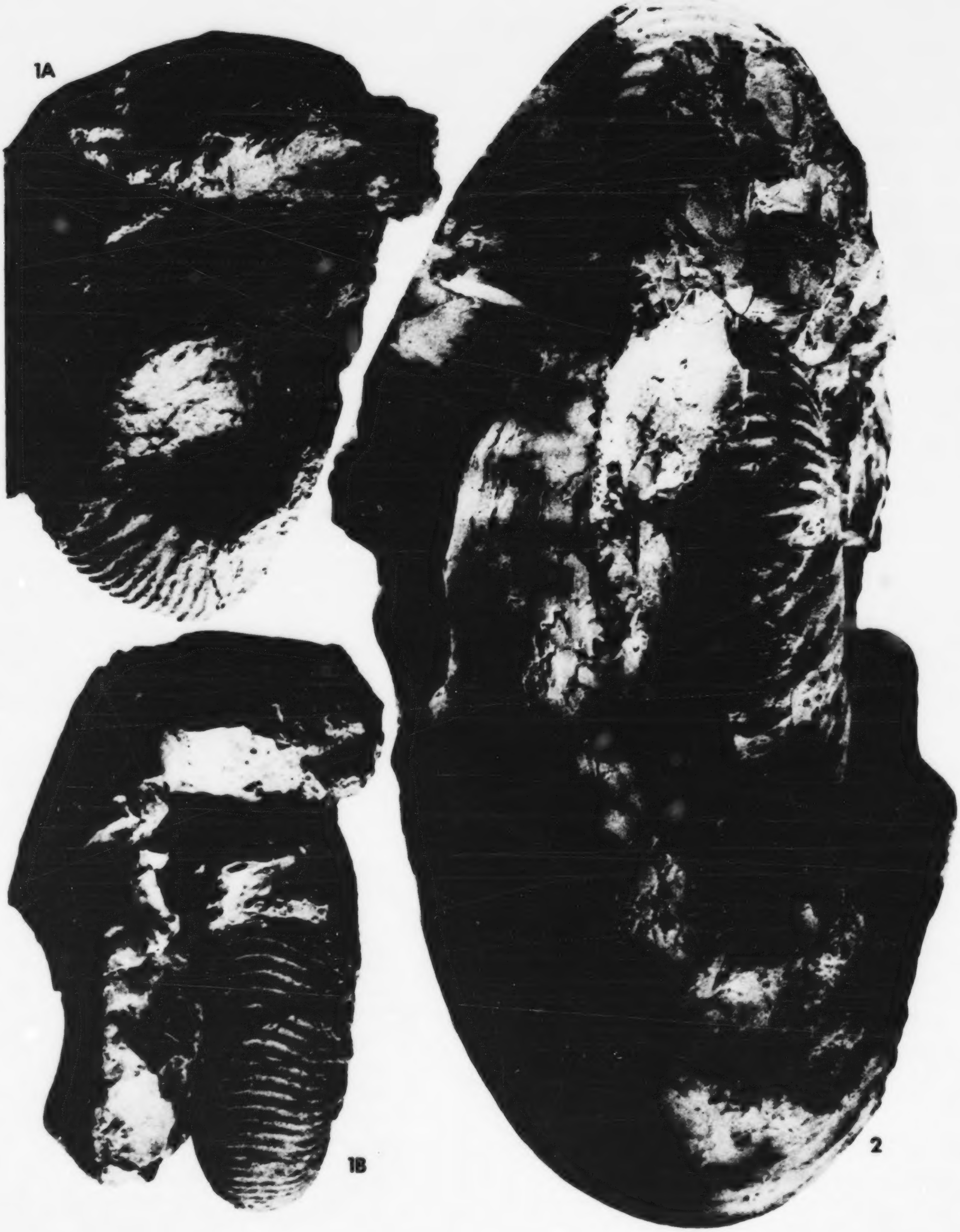

1A
1B
2

Plate 49

Figures 1A, 1B.	*Amundiptychites sverdrupi* Kemper and Jeletzky, 1979. First paratype. GSC 61765, GSC loc. 91303. View of the earlier whorls of the specimen reproduced in Pl. 48, fig. 1, x 1. 1A. Lateral view of the late juvenile and early intermediate whorls followed by a fragment of an intermediate living chamber that probably corresponds to the earlier part of of the penultimate whorl of the holotype (see Pl. 53, fig. 1). Note the contrast of the shape and ornament of these two whorls that match closely those of the equivalent whorls of the fragments reproduced in Pl. 53, fig. 2. 1B. Ventral view of the late juvenile whorl and the cross-section of the intermediate whorl reproduced in 1A.
Figures 2A-2C.	*Astieriptychites obsoletus* n. sp. Holotype. GSC 77110, GSC loc. 93865. Specimen reproduced in Pl. 42, fig. 3. 2A. Lateral view of the flank opposite to that reproduced in Pl. 42, fig. 3 with the last one-third of the whorl taken off. The surface is not whitened to exhibit well preserved external suture lines; 2B. Ventral view of the oral third of the whorl reproduced in 2A. The surface is not whitened to exhibit the ventral lobes of the sutures. 2C. Lateral view of fragments of three preceding whorls extracted from the whorl shown in 2A-2B. See Pl. 57, fig. 4E for a whitened version.
Figures 3A-3C.	*Prodichotomites* aff. *P. hollwedensis* Kemper, 1978. GSC 77118, GSC loc. 85023. Specimen reproduced in Pl. 45, fig. 2. All photographs, x 1. 3A. Lateral view of the last preserved whorl including an about three-quarter whorl long, mostly fragmentary segment of the adult living chamber. Note the rapidly progressing decline of the ornament on the flank as compared with the preceding adult penultimate whorl (see 3B); 3B. Lateral view of the opposite flank that exhibits the adult penultimate whorl and the beginning of the adult living chamber. Note the same decline of the ornament as in 3A. 3C. Ventral view of the undeformed middle third of the whorl shown in 3B. It consists of the oralmost part of the phragmocone.

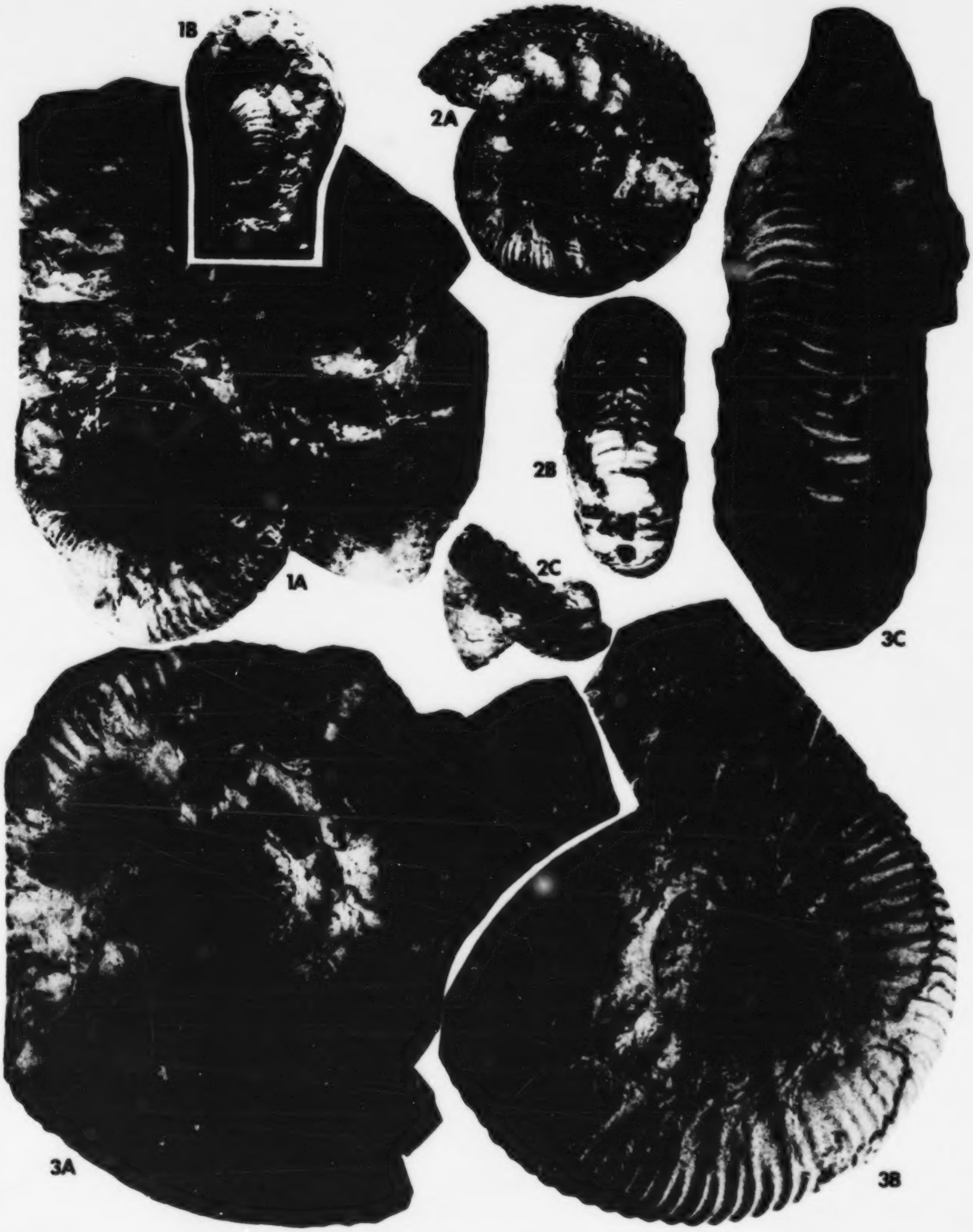
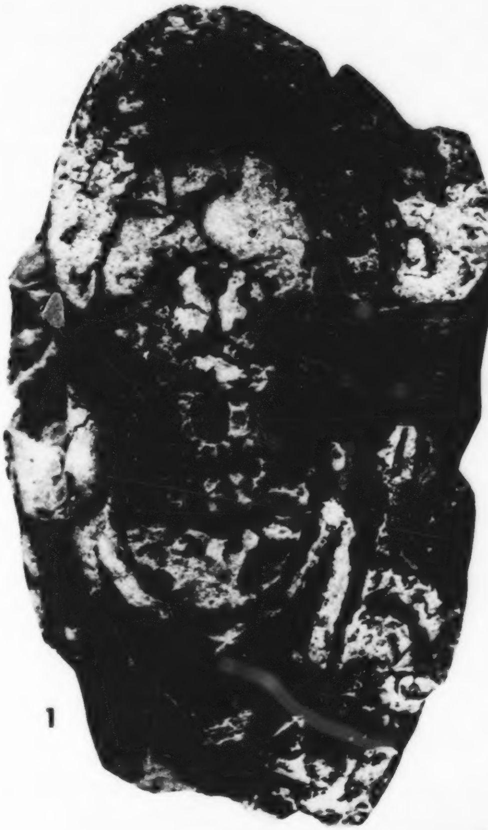

1B
2A
2B
1A
2C
3C
3A
3B

Plate 50

Figure 1 — *Ringnesiceras tozeri* Kemper and Jeletzky, 1979. Holotype. GSC 33332, GSC loc. 100800. Cross-sections of five intermediate and juvenile whorls and the imprint of the venter of the sixth early juvenile whorl, x 1.

Figures 2A-2C. — *Polyptychites balkwilli* n. sp. First paratype. GSC 77120, GSC loc. 85025. Early growth stages of the species which are not visible in the holotype (compare Pl. 44, fig. 4; Pl. 45, fig. 1). This partly deformed specimen is entirely septate. All photographs, x 1. 2A. Lateral view. Note the rapid decline of the ornament on the flank of the oral half of the whorl which is coupled with equally rapid increase in spacing and size of the umbilical bullae. 2B. Lateral view of the other flank that exhibits the same oralward changes of the ornament. Note excellently preserved external suture lines. 2C. Ventral view of the earliest third of the whorl where the ribbing is still prominent. Note the excellently preserved ventral parts of the suture lines.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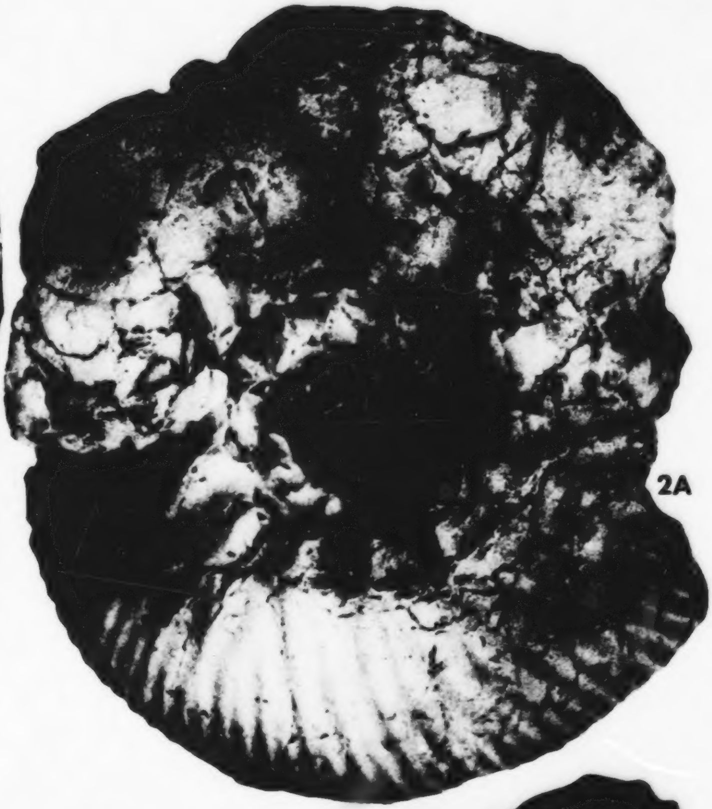
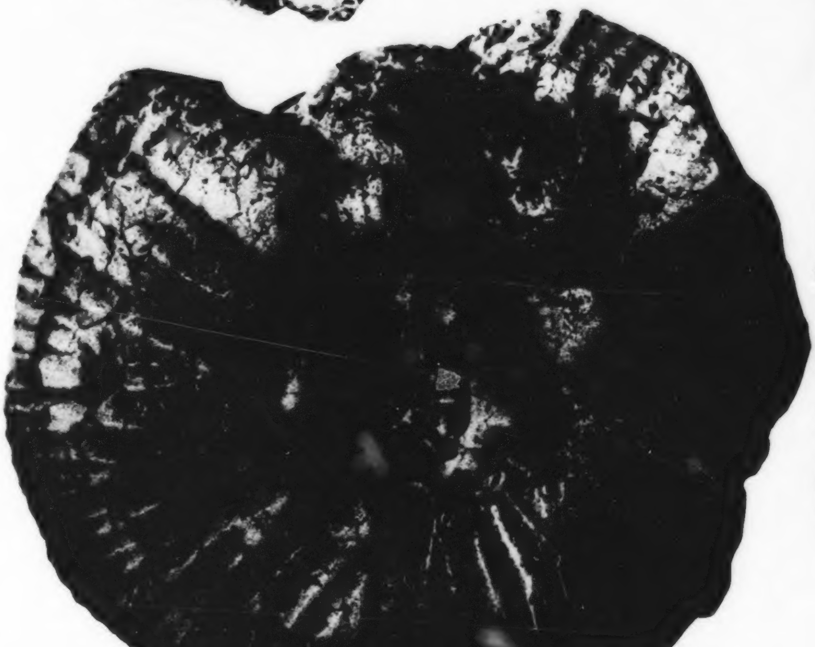

2A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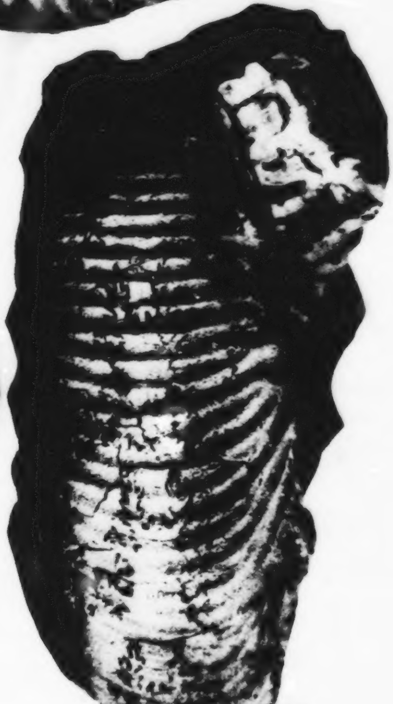

2C

Plate 51

Figures 1A-1D. *Ringnesiceras tozeri* Kemper and Jeletzky, 1979. Holotype. GSC 33332, GSC loc. 100800. The same specimen as in Pl. 50, fig. 1. All photographs x 1. Views of fragments of the two last preserved whorls of the holotype, which appear to represent parts of the second and third adult penultimate whorls respectively. 1A. Lateral view of the last preserved whorl with the short segment of the preceding whorl visible. Note the excellently preserved external suture lines drawn in Figure 61d. 1B. Lateral view of the other flank where the well preserved sculpture of the preceding whorl is well exposed; 1C. Terminal cross-section of the outermost preserved whorl and the oblique ventral views of short segments of two preceding whorls; 1D. Oblique ventral view of the last preserved whorl and the view into the venter of the preceding whorl. Note the strong decline of ribbing on the venter of the last preserved whorl in comparison with the preceding whorl. The pronounced and narrow forward bends of the secondaries on the venter are diagnostic of the species.

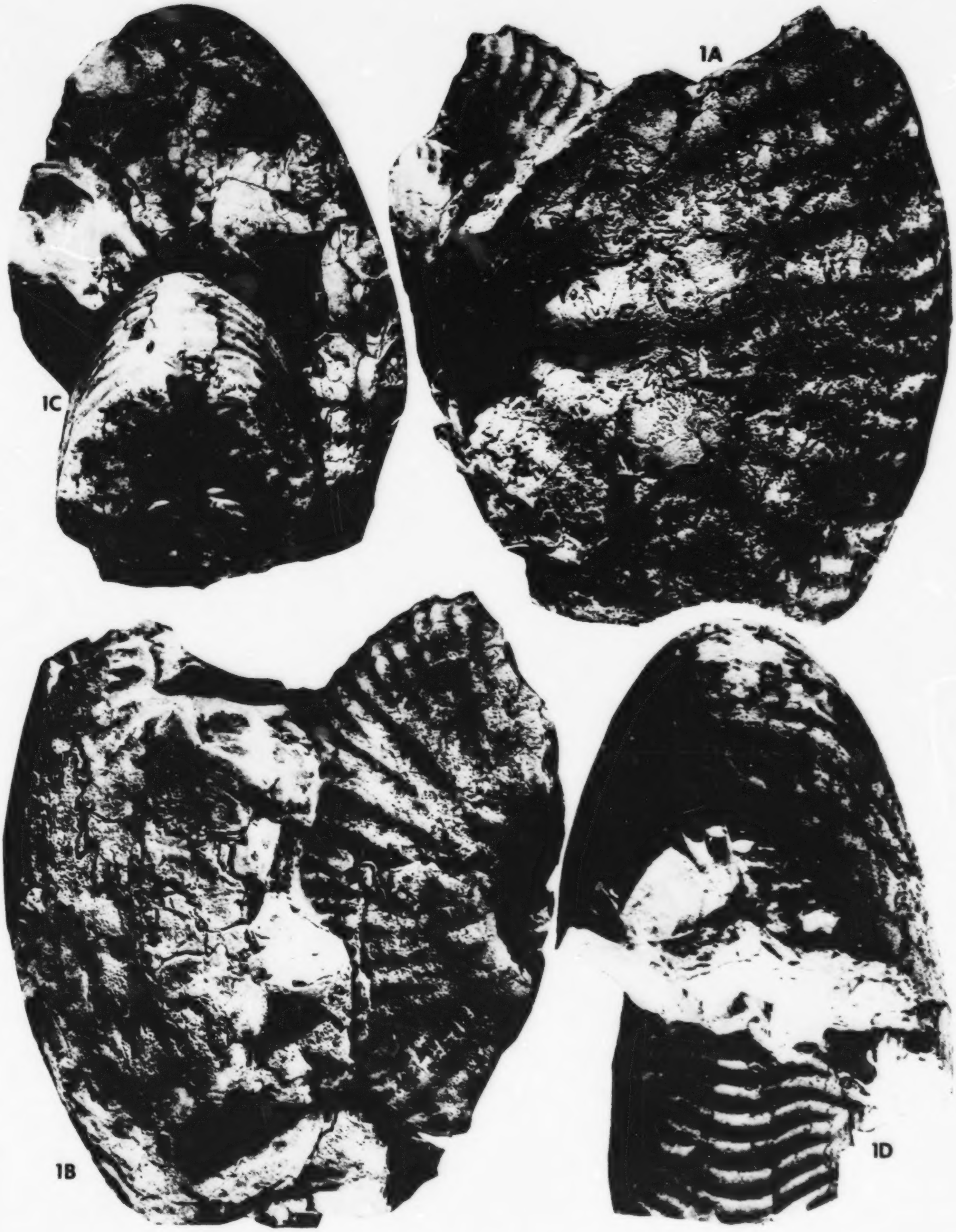

1C
1A
1B
1D

Plate 52

Figures 1A-1F.	*Polyptychites* n. sp. A. GSC 77121, GSC loc. 91301. This unique, fragmentary and fully septate representative is believed to represent intermediate whorls of a much larger *Polyptychites* form. All photographs, x 1. 1A. Lateral view of the last preserved whorl; 1B. Ventral view of the same; 1C. Lateral view of a segment of the preceding whorl with a fragment of the outermost preserved whorl still attached (see 1E); 1D. Cross-section of apical end of the segment shown in 1C and that of the next younger whorl that has much wider and lower, regularly *Euryptychites*-like cross-section; 1E. Ventral view of the same whorl segment. Note the fragment of the outermost preserved whorl still attached to its right flank; 1F. Cross-section of the oral end of this segment where the still much wider and lower cross-section of the preceding whorl begins to acquire a higher and more narrow venter characteristic of the later growth stages.
Figures 2A-2C.	*Ringnesiceras tozeri* Kemper and Jeletzky, 1979. GSC 61759, GSC loc. 91297. A juvenile specimen that exhibits the beginning of the *Simbirskites*-like sculptural stage at its oral end, x 1. 2A. Lateral view; 2B. Lateral view of the other flank, 2C. Ventral view of the oral half of the whorl.
Figures 3A-3C.	*Ringnesiceras tozeri* Kemper and Jeletzky, 1979. GSC 61760, GSC loc. 91297. A juvenile specimen that exhibits the beginning of the simbirskitinid sculptural stage at is oral end, x 1. 3A. Lateral view; 3B. Lateral view of the other flank that displays the *Simbirskites*-like primary ribs particularly clearly; 3C. Terminal cross-section and ventral view of the early half of the whorl.

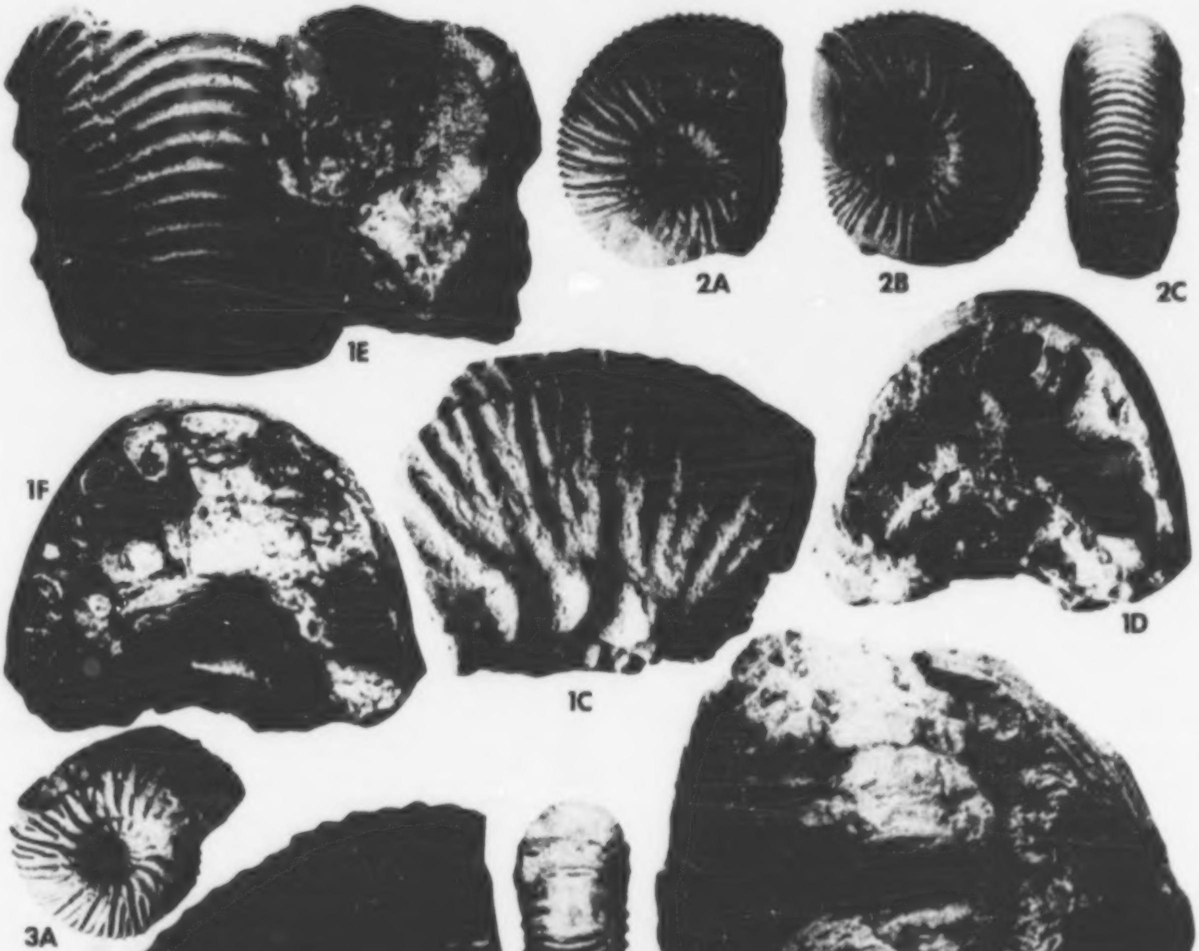

1E
2A
2B
2C
1F
1C
1D
3A
3C
3B
1B
1A

Plate 53

Figure 1	*Amundiptychites sverdrupi* Kemper and Jeletzky, 1979. Holotype. GSC 61761, GSC loc. 93753. Lateral view, x 0.9.
Figures 2A-2E.	*Amundiptychites sverdrupi* Kemper and Jeletzky, 1979. Fourth paratype. GSC 77122, GSC loc. 85059. Fragments of two early whorls (internal moulds) of the specimen that appears to be morphologically transitional to *A.* aff. *A. sverdrupi* reproduced in Pl. 47, fig. 1, x 1. 2A. Lateral view of the outer whorl; 2B. Lateral view of the other flank of that whorl; 2C. Ventral view of the same whorl; 2D. Ventral view of the inner whorl; 2E. Lateral view of the inner whorl. The lower flanks and the umbilical shoulder are broken off.

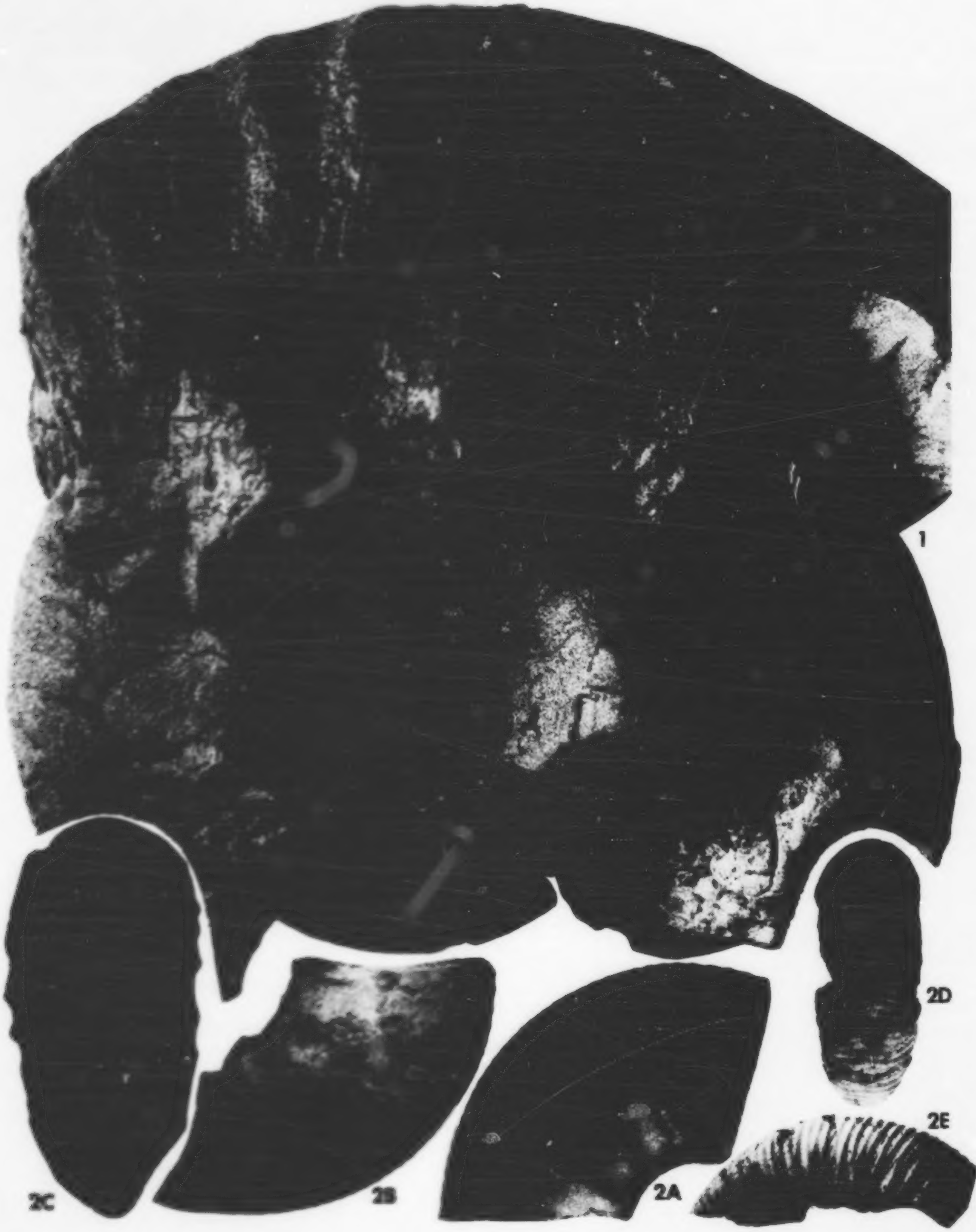
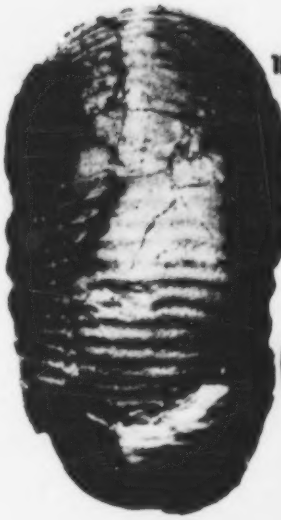

1
2D
2E
2C
2B
2A

Plate 54

Figures 1A-1B. *Siberiptychites* (*Siberiptychites*) *stubendorffi* (Schmidt, 1872). GSC 77116, GSC loc. 91310. The same specimen as in Pl. 44, fig. 3, x 1. 1A. Lateral view of the flank opposite that reproduced in Pl. 44, fig. 3. This flank lacks any pathological features and exhibits the normal ornamentation throughout; 1B. Ventral view of the oral half of the whorl. The pathological swelling is visible in the right lower corner of this photograph.

Figures 2A, 2B. *Amundiptychites sverdrupi* Kemper and Jeletzky, 1979. Holotype. GSC 61761, GSC loc. 93753. The same specimen as in Pl. 53, fig. 1, x 0.9. 2A. Cross-section of four advanced whorls and the ventral view of the fifth inner whorl that is covered by the segment of the fourth inner whorl in Pl. 53, fig. 1 and Pl. 66, fig. 2. Note the pronounced change of the whorl shape and proportions of these two whorls that is diagnostic of the genus *Amundiptychites* in general and *A. sverdrupi* in particular; 2B. Lateral view of the umbilicus and that of the fifth inner whorl with its characteristic bundling habit.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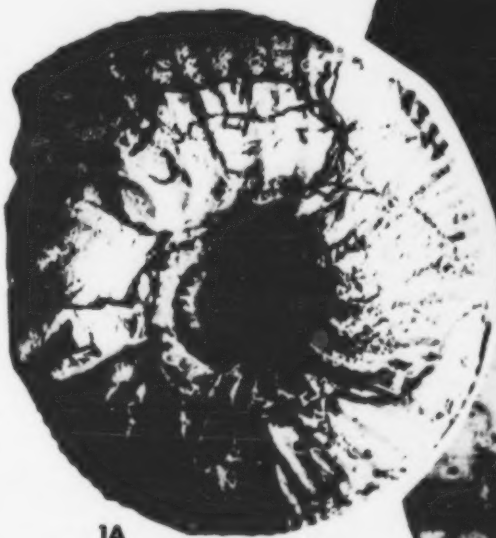
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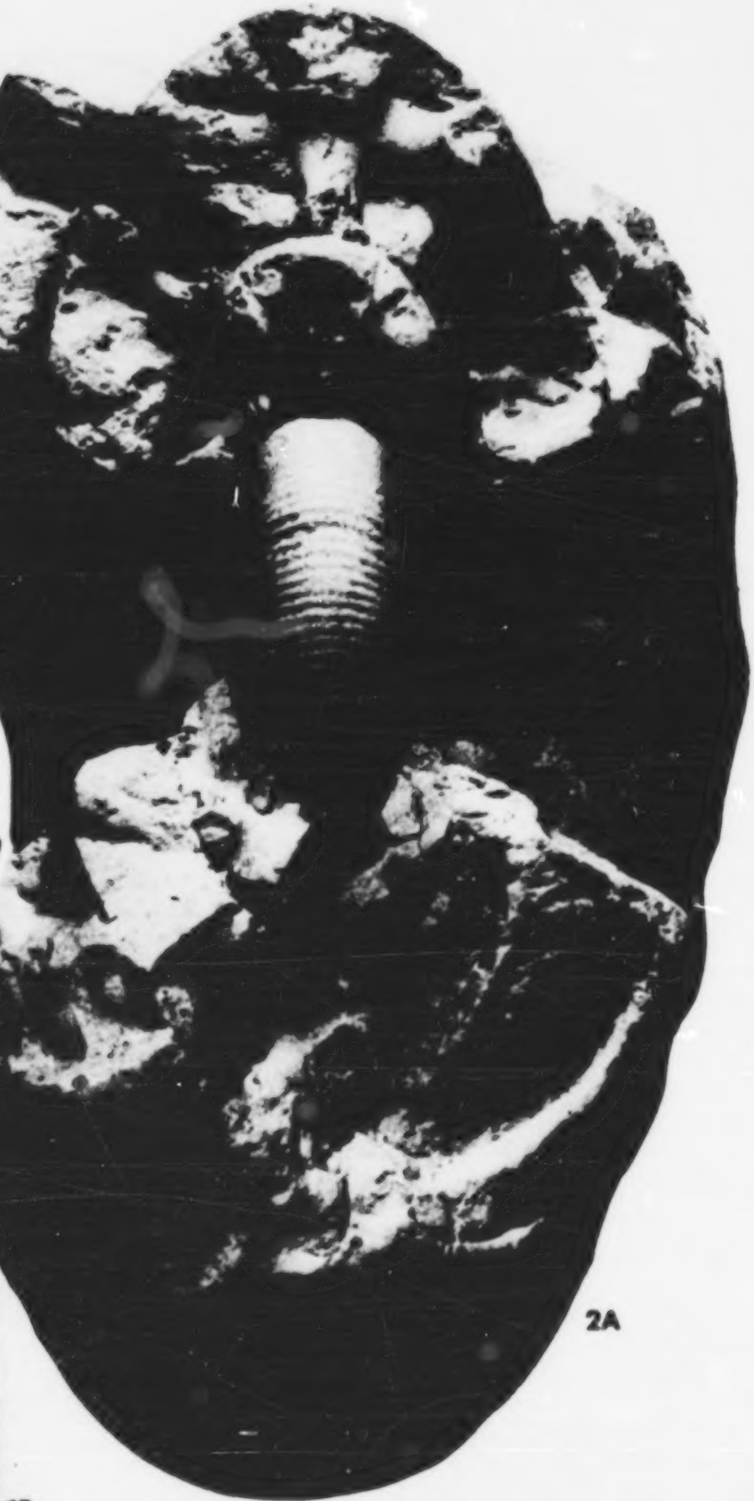

2A

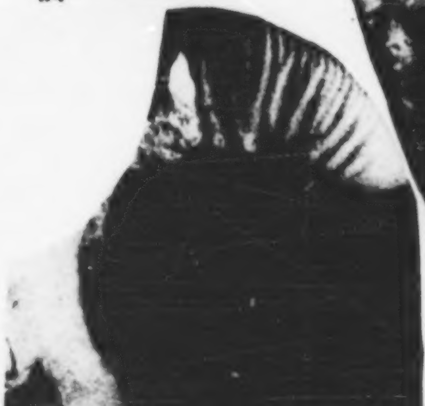

2B

Plate 55

Figures 1A, 1B. *Astieriptychites* sp. indet. A. GSC 77123, GSC loc. 91354, x 1. An almost flattened and distorted intermediate whorl. 1A. Lateral view; 1B. Lateral view of the other flank.

Figures 2A-2D. *Amundiptychites fasciatus* n. sp. Holotype. GSC 77124, GSC loc. 93867, x 1. A wholly septate, intermediate whorl. 2A. Lateral view; 2B. Lateral view of the other flank that exhibits the oralmost quarter of the preceding whorl; 2C. Terminal cross-section and ventral view of the early half of the whorl; 2D. Ventral view of the oral half of the whorl.

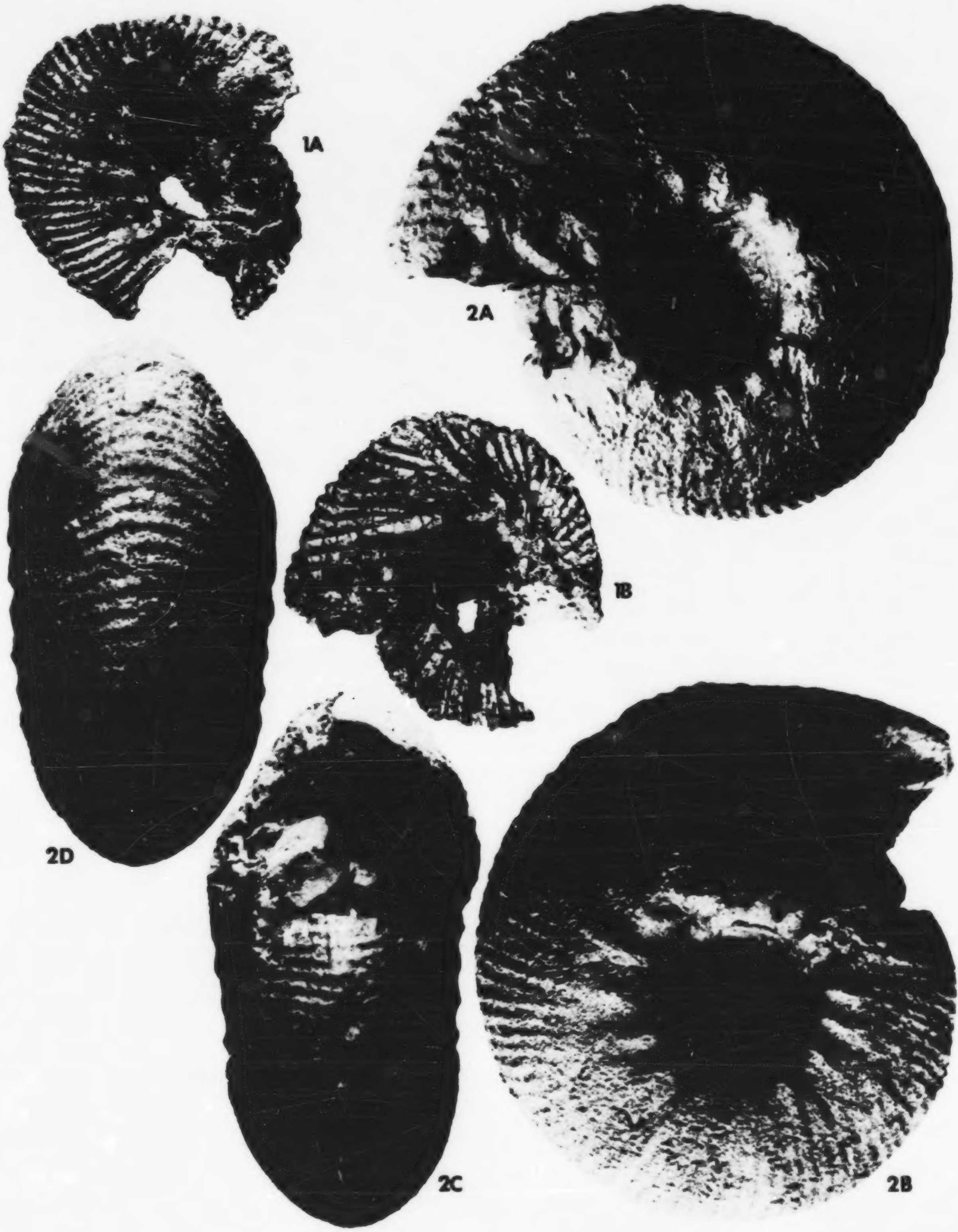
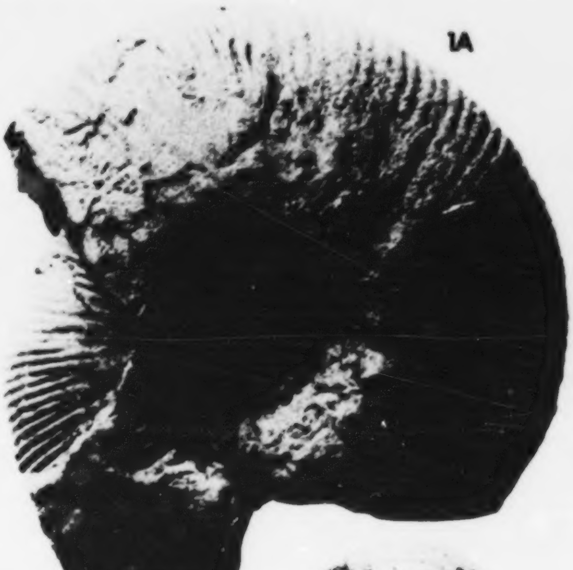
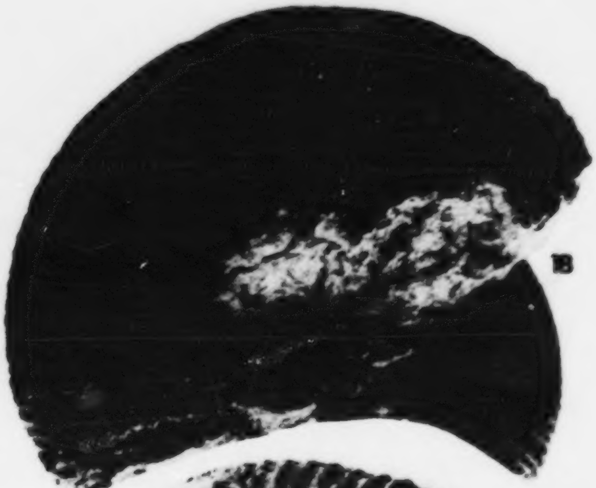

1A
2A
1B
2D
2C
2B

Plate 56

Figures 1A-1D. *Amundiptychites thorsteinssoni* n. sp. Paratype. GSC 77125, GSC loc. 93753, x 1. Intermediate whorl characterized by much more closely spaced and refined ornament than the advanced whorls (compare Pl. 61, fig. 2A). 1A. Lateral view; 1B. Lateral view of the other flank; 1C. Ventral view of the oral half of the whorl. 1D. Deformed terminal cross-section and ventral view of the early part of the whorl.

Figures 2A-2C. *Amundiptychites fasciatus* n. sp. Paratype. GSC 77126, GSC loc. 93753, x 1. A wholly septate intermediate whorl closely matching the holotype (Pl. 55, fig. 2) in its shape and proportions but strongly weathered. 2A. Lateral view. Note the deeply weathered suture lines. Only the oralmost flank is not appreciably weathered. 2B. Lateral view of the other flank that is somewhat less weathered; 2C. Ventral view of the oral half of the whorl.


1A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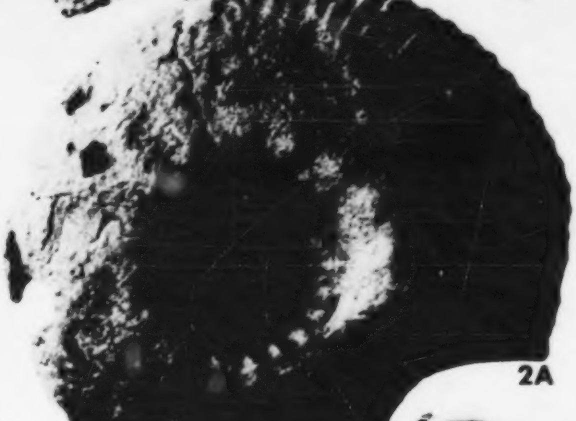
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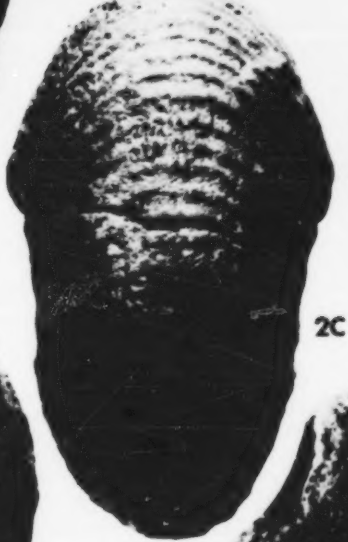
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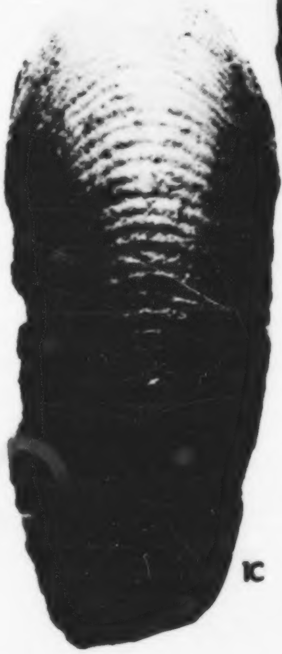
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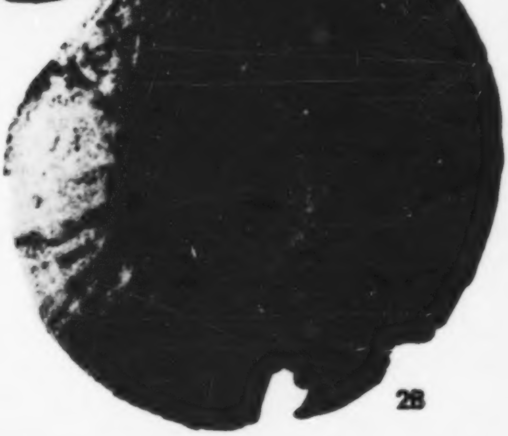
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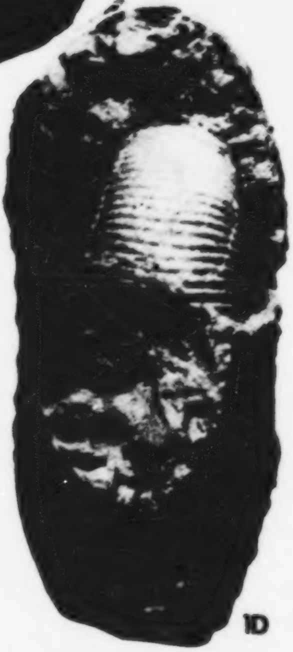

1D

Plate 57

Figure 1. *Ringnesiceras* (*Ringnesiceras*) *pseudopolyptychum* Kemper and Jeletzky, 1979. Holotype. GSC 61758, GSC loc. 93871. This specimen is also shown in Pl. 58, figs. 4A, 4B. Terminal cross-section and ventral view of the early half of the whorl of the only specimen that includes the early part of an ?intermediate living chamber, x 1.

Figure 2 *Ringnesiceras* (*Ringnesiceras*) *pseudopolyptychum* Kemper and Jeletzky, 1979. Paratype. GSC 77127, GSC loc. 93870. Lateral view of the specimen that is larger than the holotype but still fully septate (see Pl. 58, fig. 1 for ventral view). Unlike the holotype, the primary ribs of this specimen are *Polyptychites*-like, x 1.

Figure 3 *Ringnesiceras* (*Ringnesiceras*) *amundense* Kemper and Jeletzky, 1979. Paratype. GSC 77128, GSC loc. 93755. Other views of this specimen are shown in Pl. 58, figs. 3A, 3B. Terminal cross-section and ventral view of the early part of the whorl, x 1.

Figure 4A-4K. *Astieriptychites obsoletus* n. sp. Holotype. GSC 77110, GSC loc. 93865. All photographs, x 1. 4A. Lateral view of the complete specimen. Opposite flank to that reproduced in Pl. 59, fig. 4. This side displays the preceding half-whorl that is completely concealed in Pl. 59, fig. 4; 4B. Ventral view of the middle part of the last preserved whorl; 4C. Lateral view of the flank shown in Pl. 59, fig. 4 but with the last preserved half-whorl removed; 4D. Terminal cross-section and ventral view of the early part of the whorl shown in 4C; 4E. Lateral view of fragments of three preceding whorls extracted from the whorl shown in 4C, 4D. The earliest whorl segment visible is in the essentially smooth sculptural stage. The intermediate whorl fragment is in the first trivirgatitpartitous sculptural stage while the last preserved whorl fragment exhibits the fasciculate and bullate adult sculptural stage; 4F. Adapical cross-section of the outer whorl fragment and ventral view of the intermediate whorl fragment shown in 4E. Not whitened to show the ventral parts of well preserved external suture lines (see 4-I for whitened view); 4G. The other flank of the fragment shown in 4E. This flank exhibits more clearly the first trivirgatitpartitious and the fasciculate to bullate sculptural stages. The innermost whorl is completely concealed; 4H. Adoral cross-sections of the outer and intermediate whorls and the ventral view of the innermost whorl shown in 4E. 4-I. The same view as in 4F but whitened to show details of very fine and dense ribbing and a constriction on the venter of the intermediate whorl; 4J. Oblique ventral view of the outer and intermediate whorl fragments shown in 4E to 4-I inclusive. Note the second constriction on the intermediate whorl and the contrast in the degree of refinement and density of secondary ribs of the intermediate and outer whorls; 4K. The same view as in 4G but not whitened to show well preserved lateral parts of external suture lines on the intermediate whorl fragment.

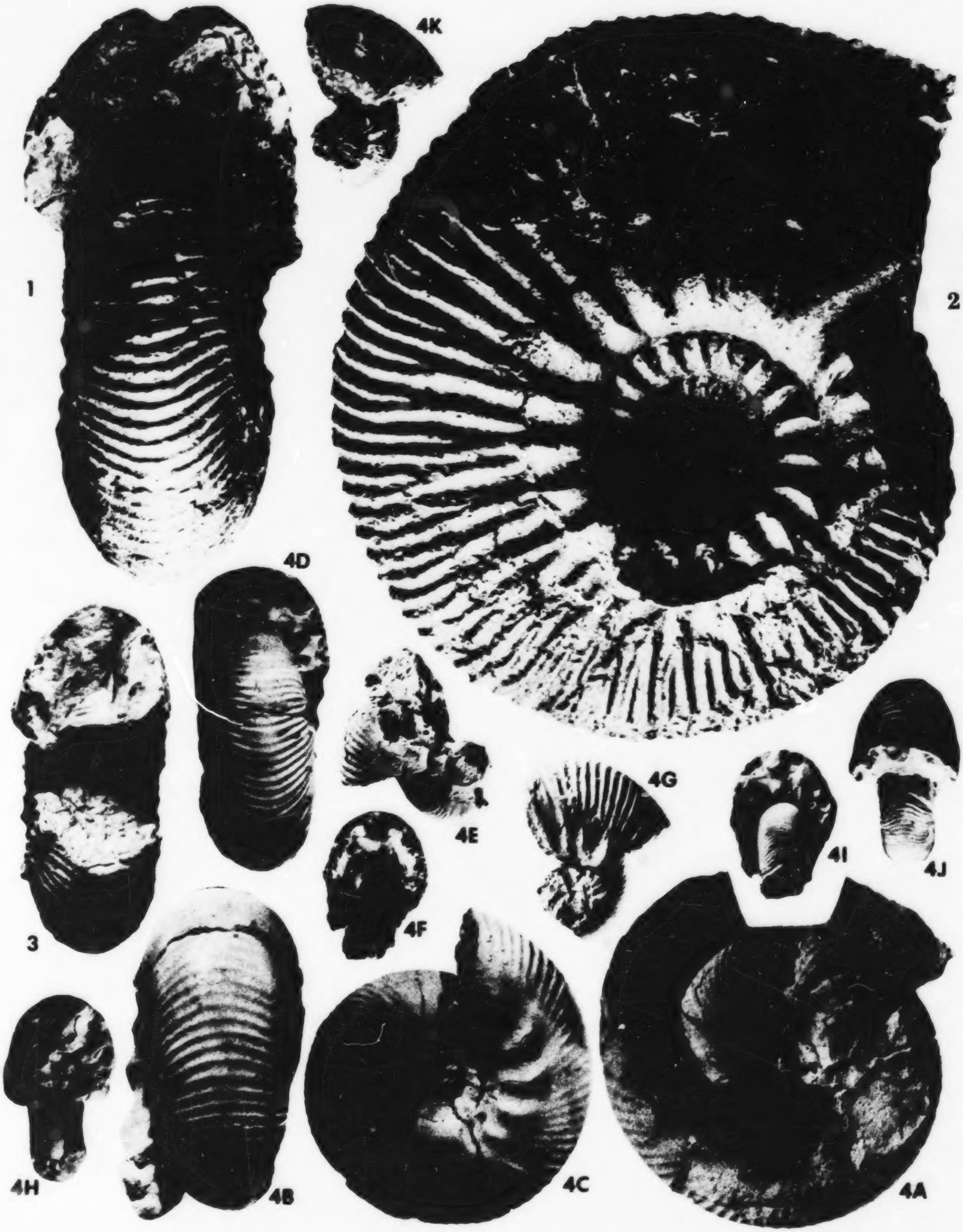
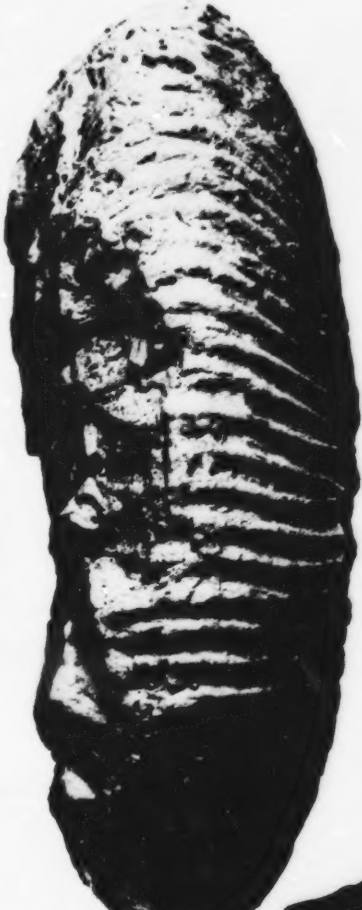

4K
1
2
4D
3
4E
4G
4I
4J
4F
4H
4B
4C
4A

Plate 58

Figure 1.	*Ringnesiceras* (*Ringnesiceras*) *pseudopolyptychum* Kemper and Jeletzky, 1979. GSC 77127, GSC loc. 93870. Ventral view of the specimen shown in Pl. 57, fig. 2, x 1.
Figures 2A-2C.	*Ringnesiceras* (*Ringnesiceras*) *amundense* Kemper and Jeletzky, 1979. Holotype. GSC 61756, GSC loc. 93755. Adult specimen with the early part of living chamber preserved (its beginning marked by an arrow), x 1. 2A. Lateral view; 2B. Lateral view of the other flank; 2C. Terminal cross-section and ventral view of the early part of the whorl.
Figures 3A, 3B	*Ringnesiceras* (*Ringnesiceras*) *amundense* Kemper and Jeletzky, 1979. Paratype. GSC 77128, GSC loc. 93755, x 1. A somewhat deformed adult specimen that includes the early part of the living chamber. This specimen differs from the holotype in its somewhat more slender whorl section and its distinctly coarser and more widely spaced ribs, x 1. 3A. Lateral view; 3B. Ventral view of the oral half of the whorl. See Pl. 57, fig. 3 for the terminal cross-section and the ventral view of the early part of the whorl.
Figures 4A, 4B.	*Ringnesiceras* (*Ringnesiceras*) *pseudopolyptychum* Kemper and Jeletzky 1979. Holotype. GSC 61758, GSC loc. 93871, x 1. 4A. Lateral view showing well developed simbirskitiform primary ribs on the earliest exposed one-third of the flank and adumbilical parts of the preceding whorls in the umbilicus; 4B. Lateral view of the other flank that shows the replacement of these simbirskitiform primaries by comma-like umbilical bullae. See Pl. 57, fig. 1 for the ventral view.



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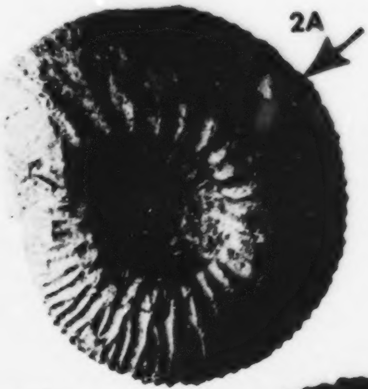

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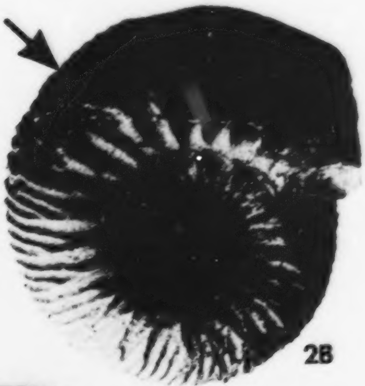

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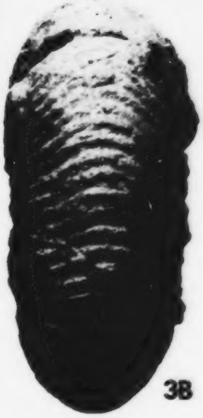

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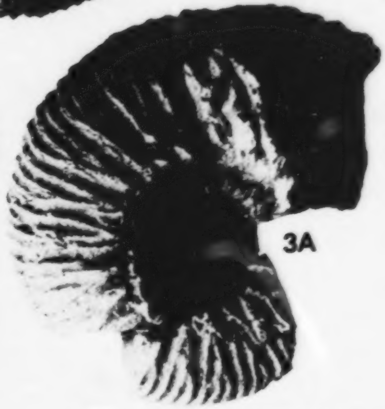
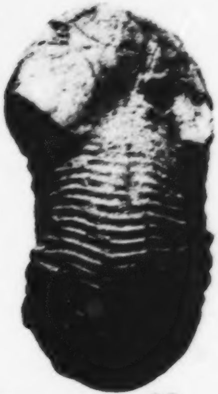


3A



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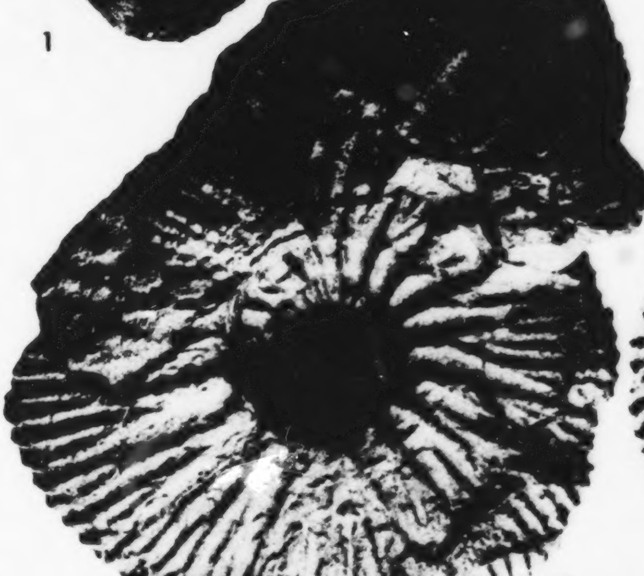
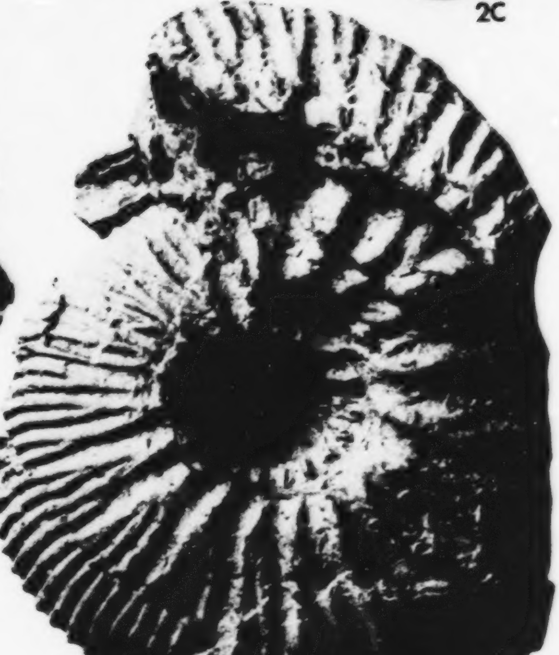


4A



4B

Plate 59

Figures 1A, 1B	*?Ringnesiceras* (*Ringnesiceras*) n. sp. aff. *R.* (*R.*) *amundense* Kemper and Jeletzky, 1979. GSC 77129, GSC loc. 93753, x 1. Wholly septate, intermediate whorl that differs from the younger *R.* (*R.*) *amundense* in its narrower cross-section. 1A. Lateral view; 1B. Terminal cross-section (deformed) and ventral view of the early half of the whorl.
Figures 2A, 2B.	*Ringnesiceras* (*Ringnesiceras*) *pseudopolyptychum* Kemper and Jeletzky, 1979. Paratype. GSC 77130, GSC loc. 93871. Fragmentary but undeformed and well preserved early and intermediate whorls that reveal details of the ontogenetic development of the species, x 1. 2A. Lateral view; 2B. Terminal cross-section of the last preserved whorl and ventral view of the preceding whorl.
Figures 3A-3C.	*Ringnesiceras* (*Ringnesiceras*) *pseudopolyptychum* Kemper and Jeletzky, 1979. Paratype. GSC 77131, GSC loc. 93870. Specimen that matches closely the holotype in its size, whorl shape and proportions, and the ornament but is entirely septate, x 1. 3A. Lateral view; 3B. Lateral view of the other flank. 3C. Terminal cross-section and ventral view of the early half of the whorl.
Figure 4.	*Astieriptychites obsoletus* n. sp. Holotype. GSC 77110, GSC loc. 93865. Lateral view of the best preserved flank of the last preserved whorl (still entirely septate) of the specimen reproduced in Pl. 57, figs. 4A-4K, x 1. See explanation of these figures for further details.

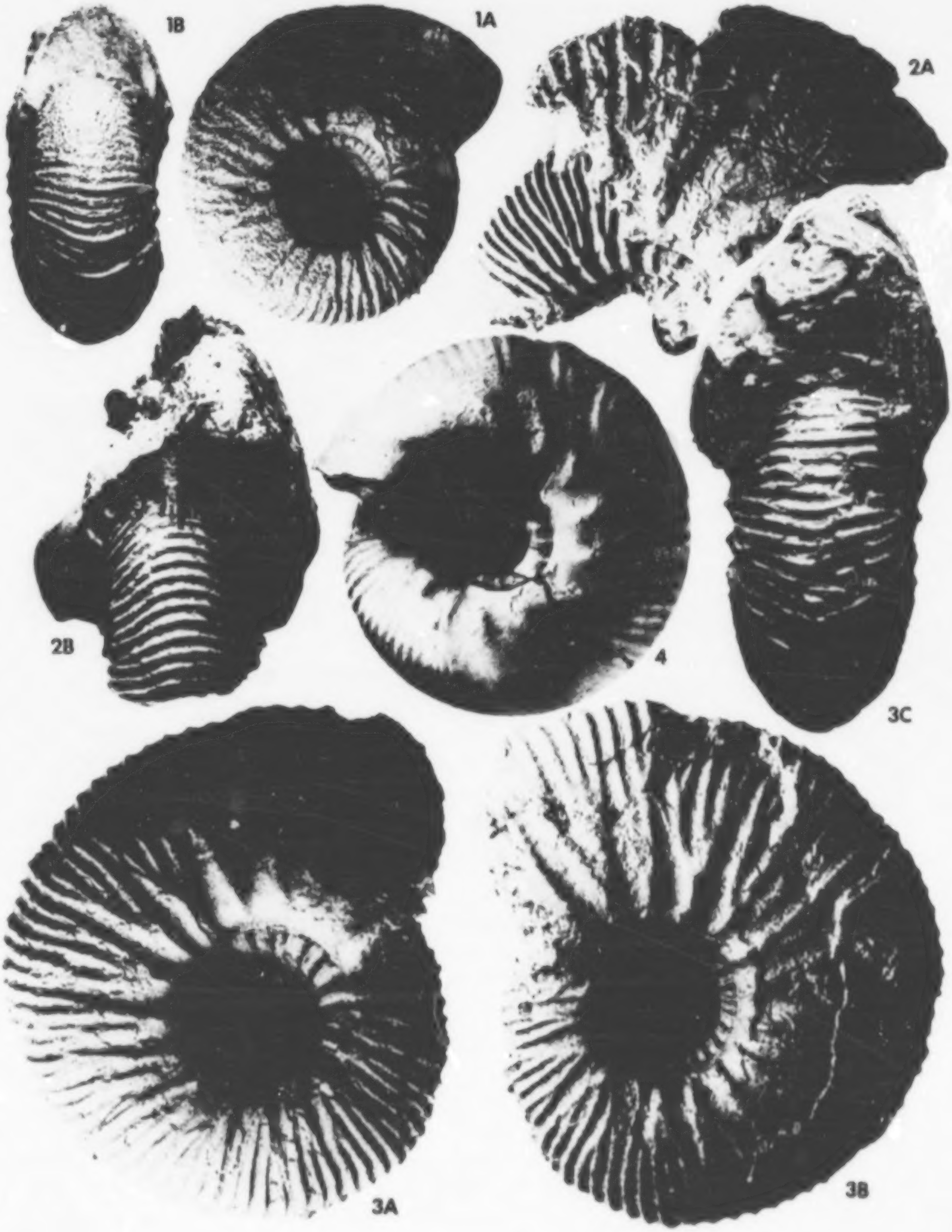

1B
1A
2A
2B
4
3C
3A
3B

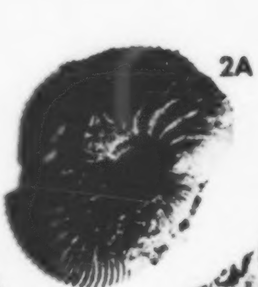
Plate 60

Figures 1A, 1B. *Ringnesiceras* (*Elleficeras*) *ellefense* Kemper and Jeletzky, 1979. Paratype. GSC 77132, GSC loc. 93868. Fragments of five juvenile and intermediate whorls. The wholly septate last preserved fragment is strongly deformed laterally, x 1. 1A. Lateral view; 1B. Lateral view of the other flank.

Figures 2A-2D *Ringnesiceras* (*Elleficeras*) n. sp. indet. juven. GSC 77133, GSC loc. 93868. A strongly damaged juvenile whorl that is nevertheless obviously considerably more slender than the equivalent whorls of the subgenus *Ringnesiceras*. All photographs x 1. 2A. Lateral view; 2B. Lateral view of the other flank; 2C. Ventral view of the oral half of the whorl; 2D. Terminal cross-section and ventral view of the early half of the whorl.

Figures 3A-3D. *Ringnesiceras* (*Ringnesiceras*) *ellefense* Kemper and Jeletzky, 1979. Holotype. GSC 61757, GSC loc. 93870, x 1. Wholly septate intermediate whorl that exhibits a segment of the preceding whorl. 3A. Lateral view; 3B. Lateral view of the other flank. 3C. Ventral view of the early third of the outer whorl; 3D. Ventral view with the middle third of the outer whorl taken off to show ventral view of the preceding whorl.

Figure 4 *Ringnesiceras* (*Ringnesiceras*) *pseudopolyptychum* Kemper and Jeletzky, 1979. Paratype. GSC 77130, GSC loc. 93871. The other lateral view of the specimen reproduced in Pl. 59, fig. 2, x 1. See descriptions of that figure and of Pl. 58, fig. 4 for further details.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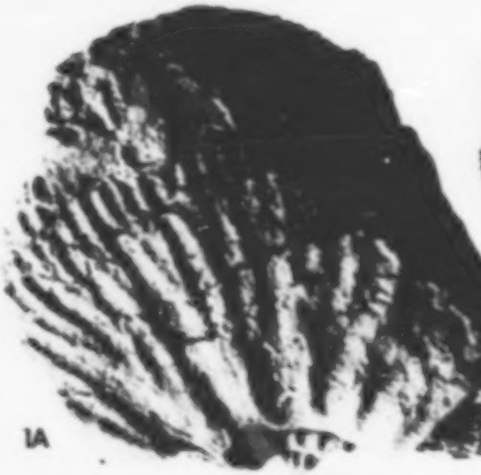
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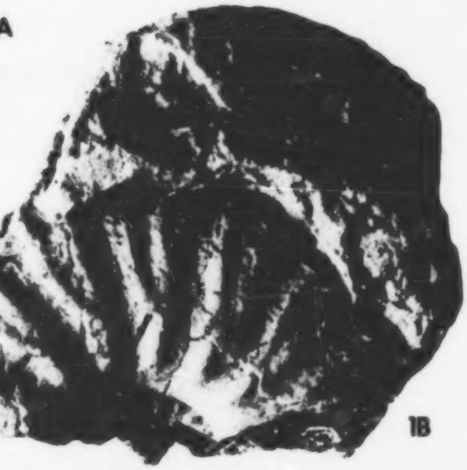
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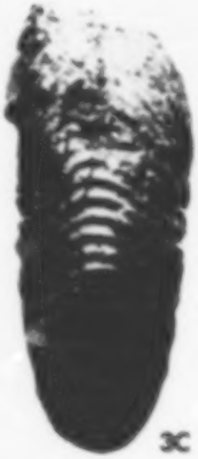
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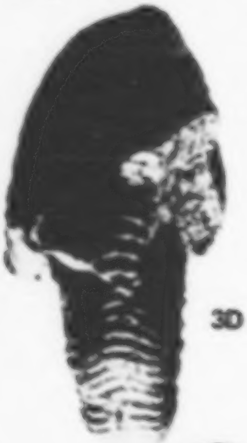
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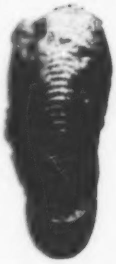
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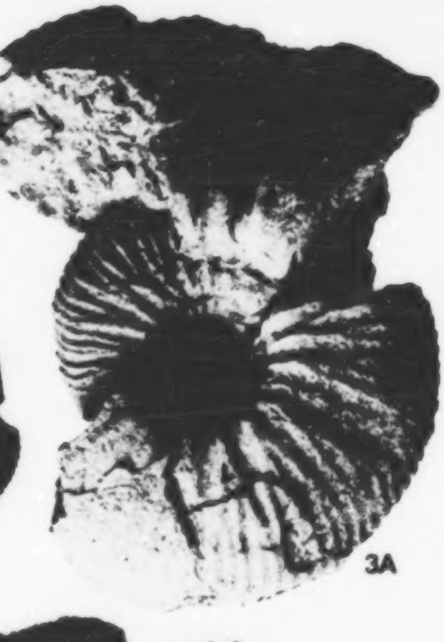
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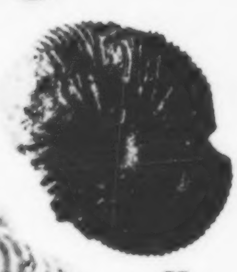
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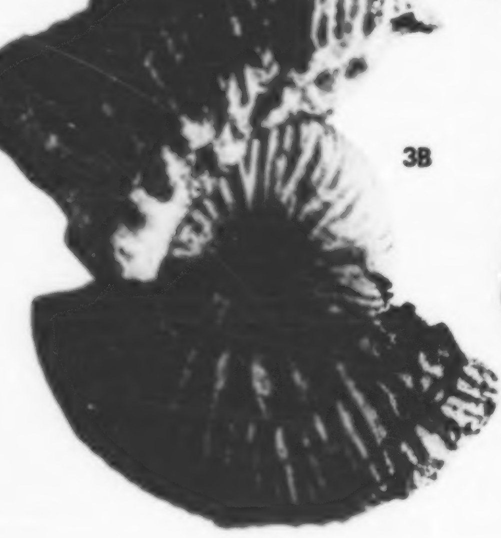
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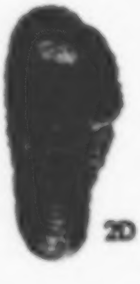
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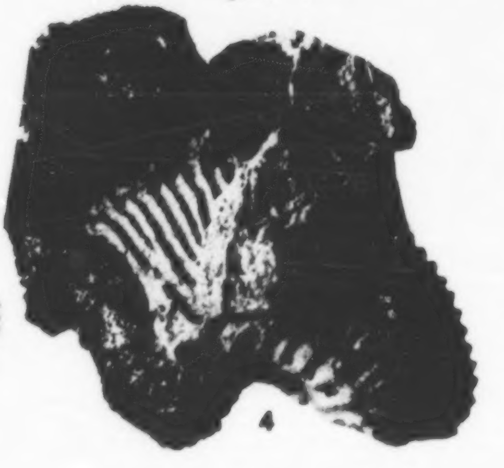

4

Plate 61

Figures 1A-1C. *Siberiptychites* (*Siberiptychites*) *fascicostatus* n. sp. Paratype. GSC 77134, GSC loc. 24024. Fragmentary specimen exhibiting an earlier whorl than that of the holotype (see Pl. 35, fig. 2). This whorl is ornamented by simple dichotomous rib bundles, x 1. 1A. Lateral view; 1B. Terminal cross-section and the ventral view of the early third of the whorl; 1C. Lateral view of the other flank ornamented exclusively by simple dichotomous rib bundles.

Figures 2A-2C. *Amundiptychites thorsteinssoni* n. sp. Holotype. GSC 77135, GSC loc. 93753. 2A. Lateral view of the complete, entirely septate specimen, x 1; 2B. Flank of juvenile whorl (fourth from the last preserved) visible in the umbilicus of 2A, x 2. Note the closely spaced and refined, mostly bidichotomous ribbing habit; 2C. Segment of the last part of the whorl shown in 2A with parts of the last two completely preserved external suture lines outlined in black, x1.

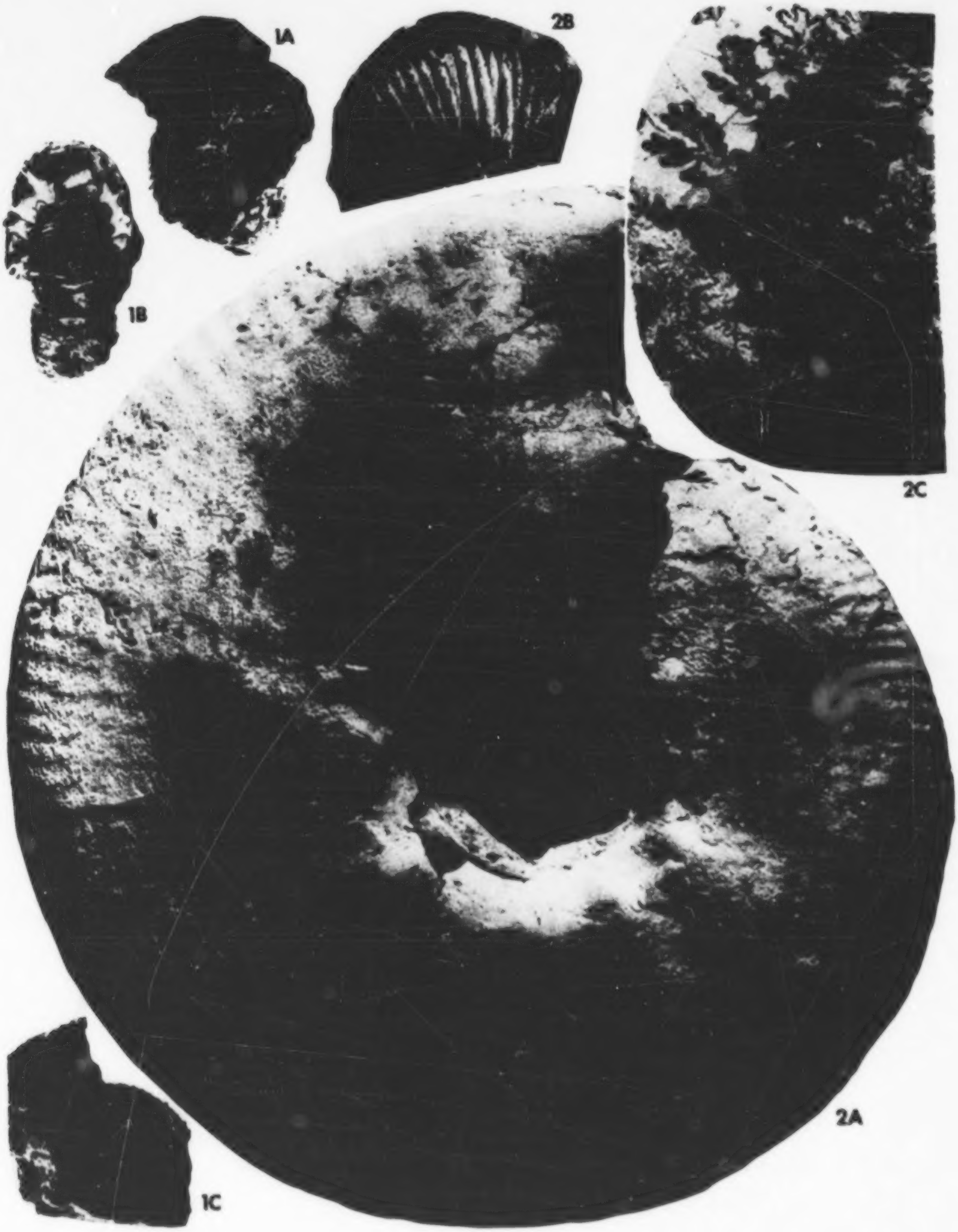
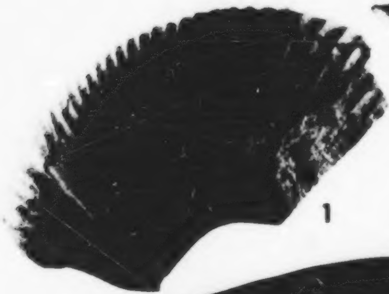

1A
2B
1B
2C
2A
1C

Plate 62

Figure 1.	*Siberiptychites* (*Siberiptychites*) n. sp. aff. *stubendorffi* (Schmidt, 1872). GSC 77136, GSC loc. 93754 (= GSC loc. 91308). Lateral view of the specimen reproduced in Pl. 63, fig. 2, x 1. Note constriction near the apical break of the fragment.
Figures 2A, 2B.	*Astieriptychites obsoletus* n. sp. Holotype. GSC 77110, GSC loc. 93865. External suture lines of the specimen reproduced in Pl. 57, fig. 4. See explanation of that figure for further details. 2A. Oblique view of adumbilical and umbilical parts of the sutures that are less clearly visible at the level about one-third of a whorl before the oral end of the specimen reproduced in Pl. 49, fig. 2A (just adorally of the break), x 2. 2B. Lateral view of the same suture lines centered at the first and second lateral lobes, x 2. See Figures 58b, 58c for camera lucida drawings of these sutures.
Figure 3	*Amundiptychites thorsteinssoni* n. sp. Holotype. GSC 77135, GSC loc. 93753. Lateral view of the other flank of the complete, entirely septate specimen reproduced in Pl. 61, fig. 2A, x 1. See explanation of that figure for further details.



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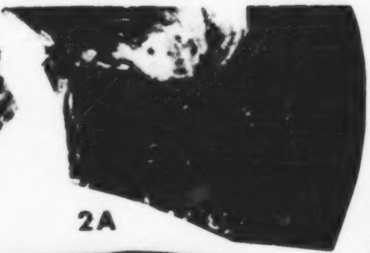
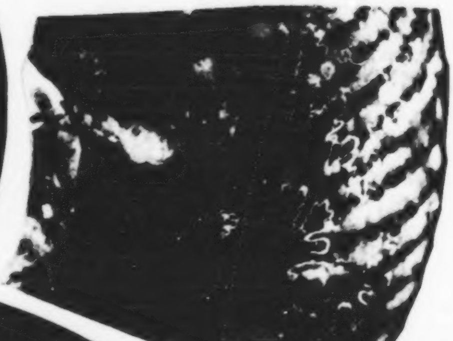


2A



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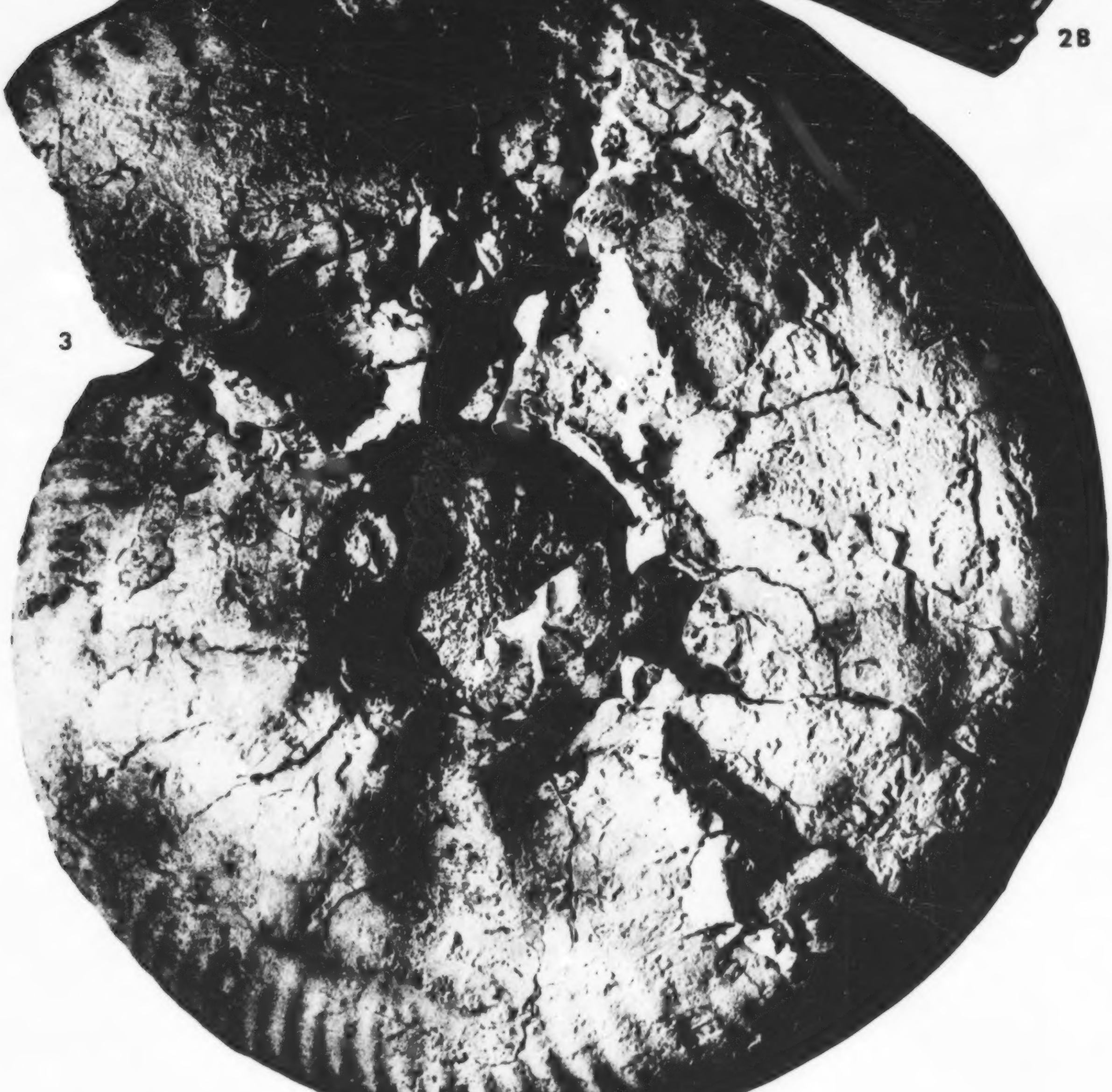


3

Plate 63

Figures 1A-1C. *Amundiptychites thorsteinssoni* n. sp. Holotype. GSC 77135, GSC loc. 93753. The specimen reproduced in Pl. 61, fig. 2, x 1. 1A. Ventral view of the early half of the last preserved whorl reproduced in Pl. 61, fig. 2A; 1B. Cross-section of the early third of the last preserved whorl, that of the preceding whorl, and the ventral view of the third whorl from the last; 1C. Lateral view of the ventral part of the third from the last whorl visible in 1B and the flank of the fourth from the last whorl in its umbilicus. See Pl. 61, figs. 2A, 2B for other views of the latter whorl.

Figures 2A-2C *Siberiptychites* (*Siberiptychites*) n. sp. aff. *stubendorffi* (Schmidt, 1872) GSC 77136, GSC loc. 93754 (= GSC loc. 91308). Well preserved fragment of a presumably intermediate living chamber displaying the characteristic bundling habit combined with the equally characteristic rounded-trapezoidal cross-section, x 1. 2A. Lateral view of the best preserved flank (see Pl. 62, fig. 1 for the lateral view of the other flank); 2B. Ventral view; 2C. Undistorted apical cross-section of the last preserved fragment and the somewhat distorted cross-sections of two preceding whorls.

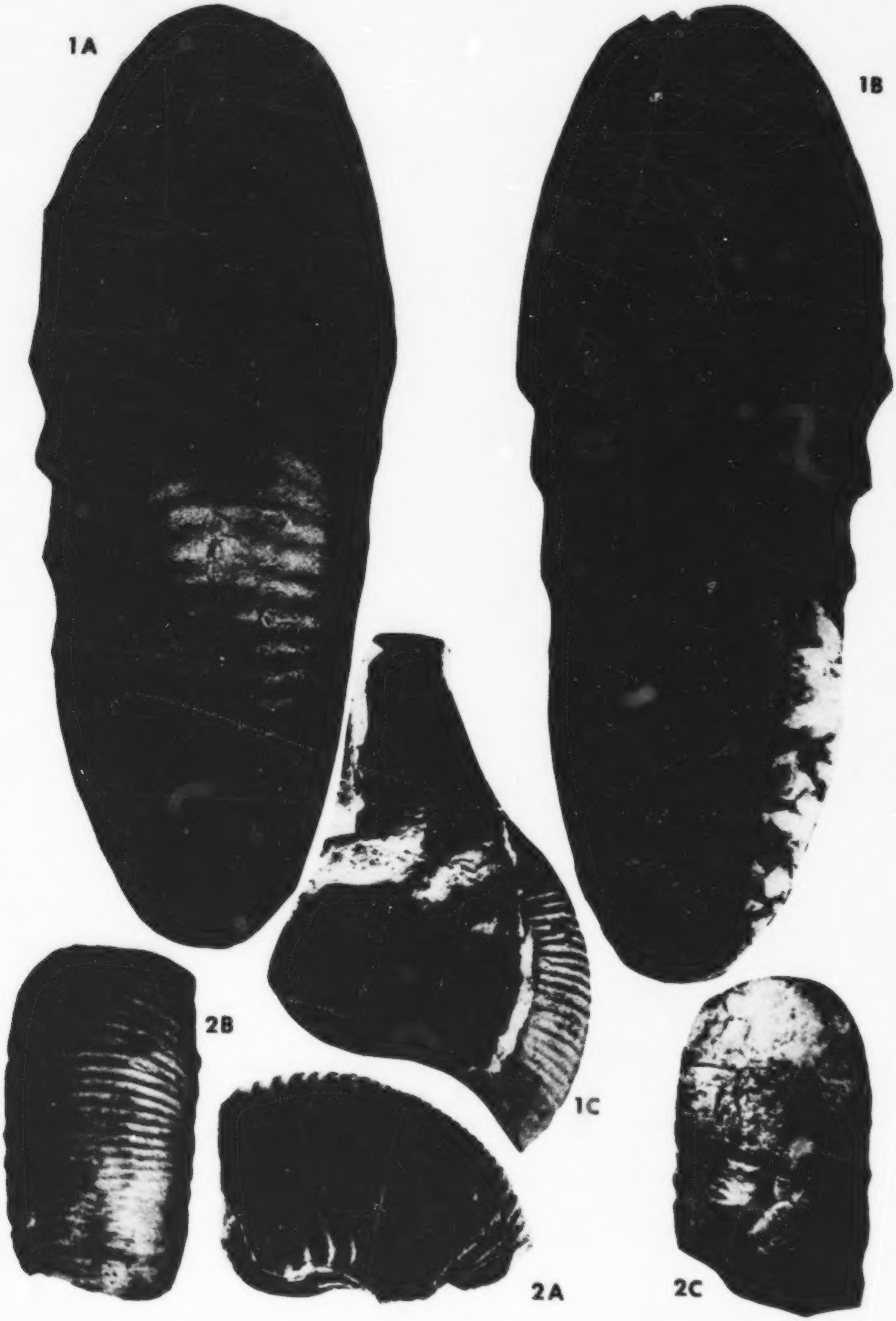
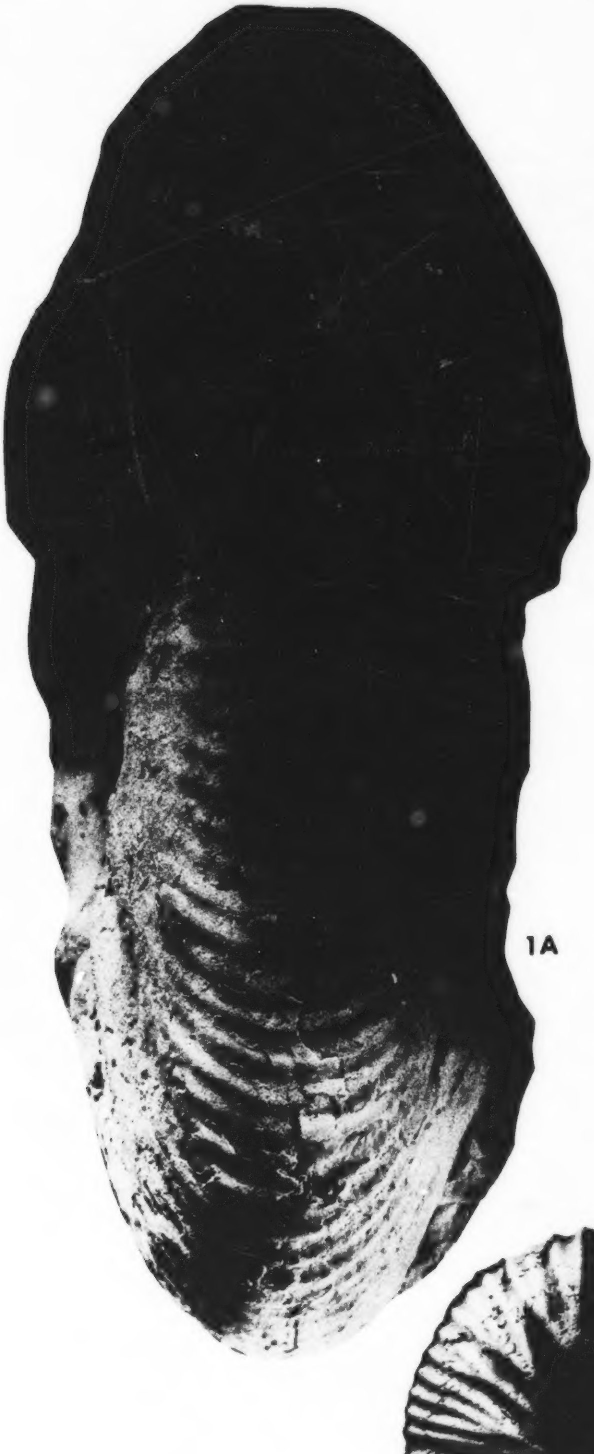

1A
1B
1C
2B
2A
2C

Plate 64

Figures 1A, 1B.	*Amundiptychites thorsteinssoni* n. sp. Holotype GSC 77135. GSC loc. 93753. The specimen reproduced in Pl. 61, fig. 2, x 1. 1A. Terminal cross-section of the complete whorl reproduced in Pl. 61, fig. 2A and ventral view of the early half of that whorl; 2B. Ventral view of the oral half of the same whorl.
Figure 2.	*Siberiptychites* (*Siberiptychites*) *stubendorffi* (Schmidt, 1872). GSC 77111, GSC loc. 91354. Lateral view of the specimen reproduced in Pl. 42, fig. 4, x 2. The enlarged view is introduced to illustrate the excellently preserved external suture lines of this specimen.



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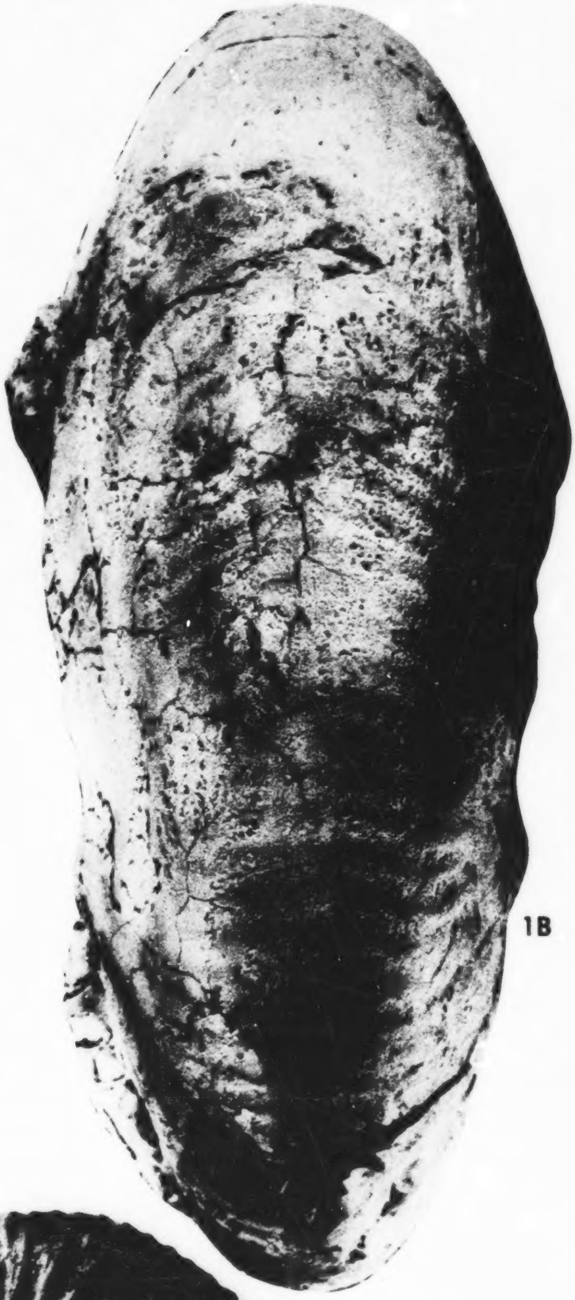

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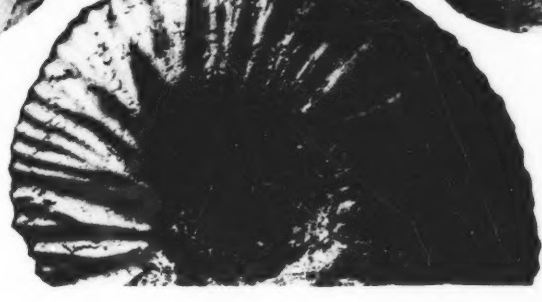


2

Plate 65

Figure 1. *Polyptychites canadensis* Kemper and Jeletzky, 1979. Paratype. GSC 77113, GSC loc. 85025. The other lateral view of the specimen reproduced in Pl. 46, fig. 2, x 0.5.

1

Plate 66

Figures 1A-1F. *Siberiptychites* (*Pseudoeuryptychites*) cf. or aff. *middendorffi* (Pavlow, 1914). GSC 77137, GSC loc. 91311. All photographs, x 1. An undeformed fragment of wholly septate, presumably penultimate whorl. 1A. Oblique apical cross-section and the inner surface of the posterior half of the specimen. Note the impression of regular ribbing of the preceding whorl on that inner surface representing an internal mould of the venter; 1B. Oblique view of the umbilical wall and umbilical shoulder visible on the right side of 1A. Note the characteristically rounded and low appearance of umbilical nodes and the prominent but still rounded appearance of the umbilical shoulder. 1C. A nearly straight view into the apical cross-section that is reproduced in an oblique view in 1A to give an idea of its true shape and proportions. The siphuncle is visible near the mid-lower margin. Note also the diagnostic presence of the first and second auxiliary lobes (outlined in black) on the preserved part of the umbilical wall in the right upper part of the photograph; 1D. Ventral view of part of the fragment shown from inside in 1A. Note the strong decline of the ornament in comparison with the preceding whorl shown in 1A; 1E. The same view as in 1D but not whitened to show the well preserved ventral and first lateral lobes; 1F. View into the flank of the fragment reproduced in 1C, 1D and 1E to show well developed first and second lateral lobes (outlined in black). The outer flank of the second auxiliary lobe is superimposed on the umbilical shoulder near the left margin of the photograph.

Figure 2 *Amundiptychites sverdrupi* Kemper and Jeletzky, 1979. Holotype. GSC 61761, GSC loc. 93753. The same specimen as in Pl. 53, fig. 1. Cross-section of the three advanced whorls and ventral view of a segment of the fourth (i.e. innermost) whorl visible in lateral aspect in Pl. 53, fig. 1. The fifth inner whorl shown in Pl. 54, figs. 2A, 2B is concealed by the fourth whorl, x 0.9.

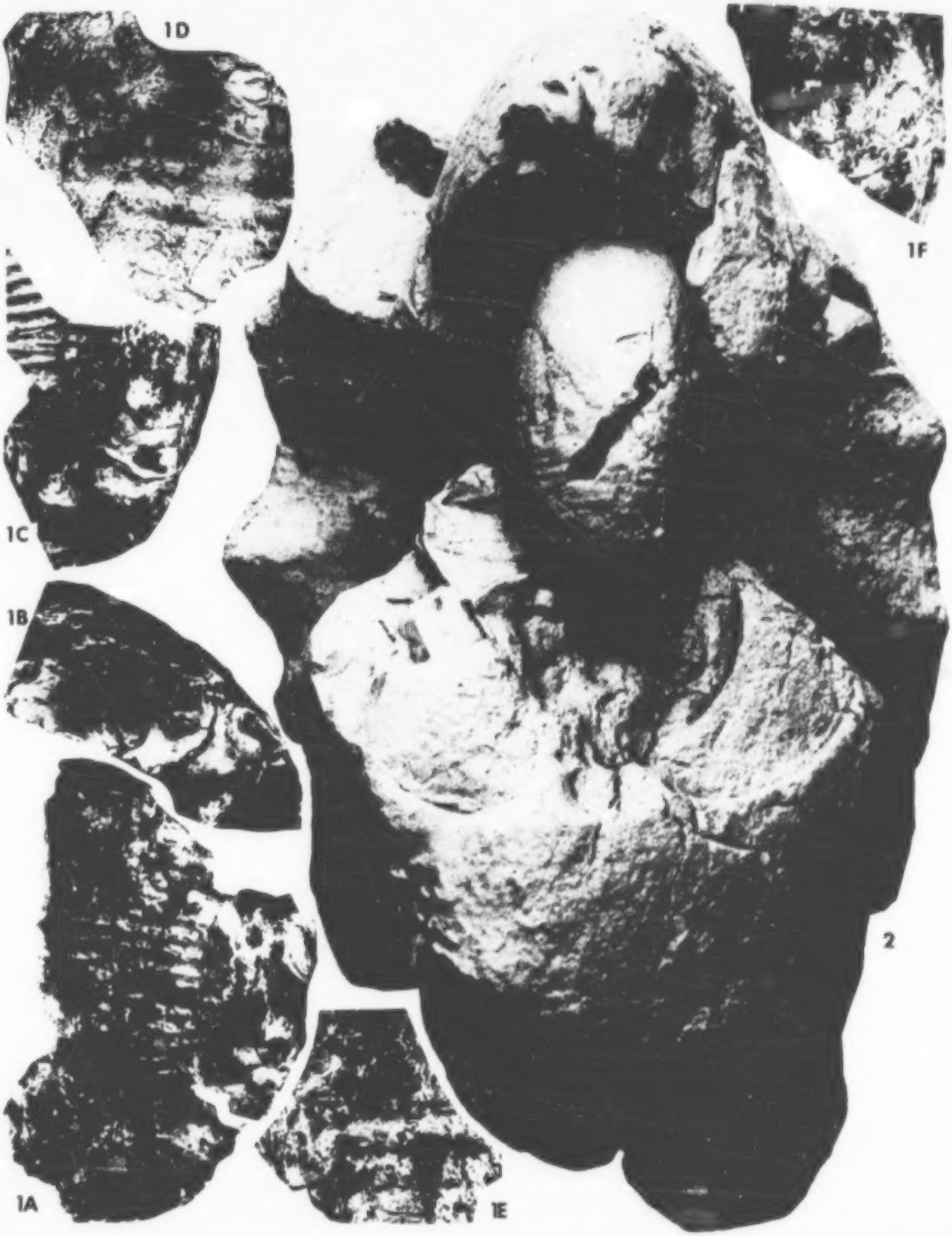
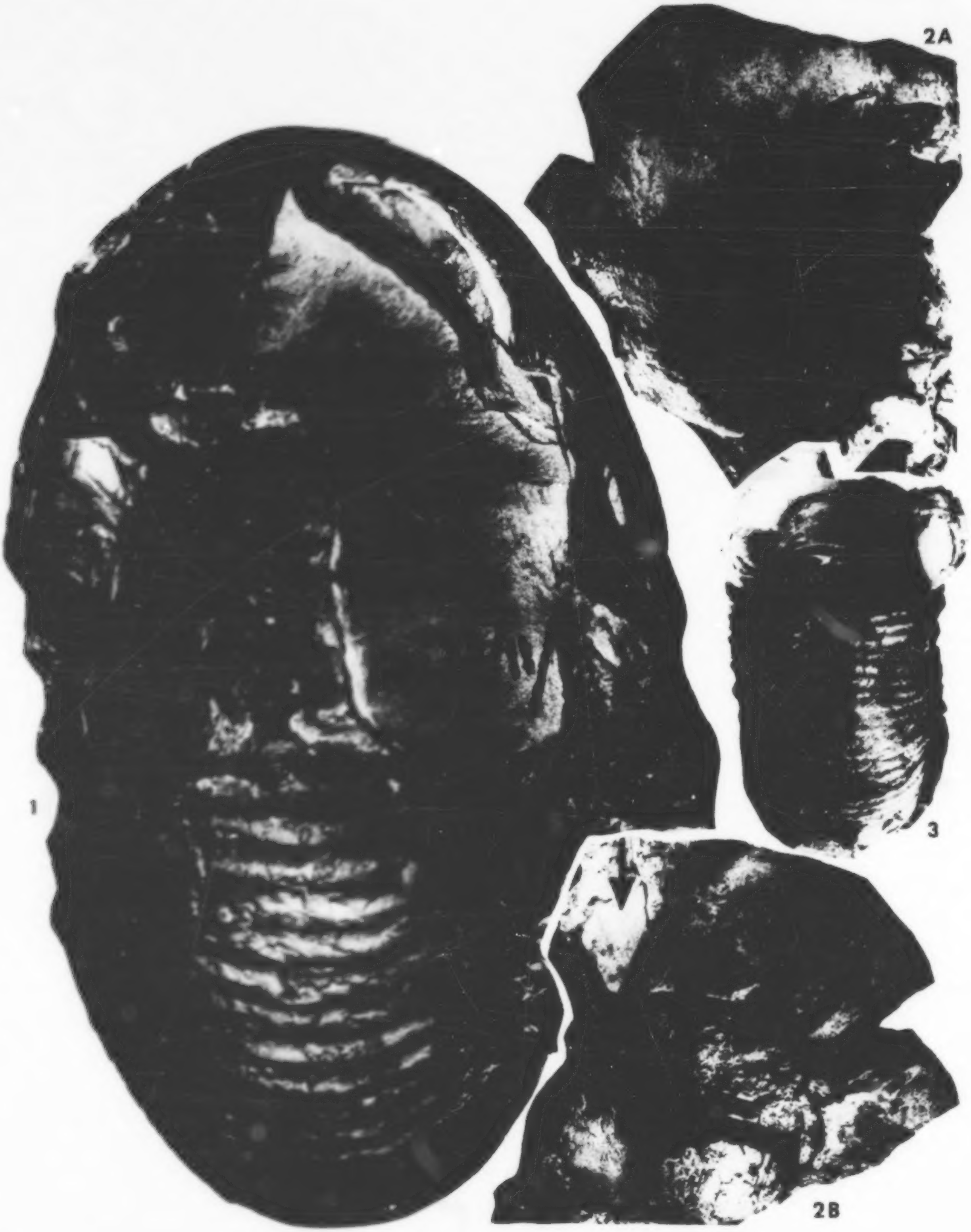

1D
1F
1C
1B
2
1A
1E

Plate 67

Figure 1. *Polyptychites tschekanovskii* Pavlow, 1914. GSC 77109, GSC loc. 91302. Ventral view of the specimen reproduced in Pl. 40, fig. 1. Terminal cross-section (undeformed) of the penultimate preserved whorl and ventral view of its early third, x 1. The fragmentary last preserved whorl (see Pl. 41, fig. 1; Pl. 42, fig. 2) superimposed on this whorl is only visible in part on the numbered right flank of the photograph.

Figures 2A, 2B. *Siberiptychites* (*Pseudoeuryptychites*) sp. indet. A. GSC 77119, GSC loc. 93754 (= 91308), x 1. 2A. Ventral view of a fragment of an apparently smooth, adult ultimate whorl. An obliquely oriented segment of sharp and bullate (two bullae only) umbilical shoulder is visible on the lower left. This umbilical shoulder is also visible on the lower right side of 2B. A small segment of evenly and coarsely ribbed penultimate whorl (also shown in Pl. 46, fig. 1) is visible on the lower right side of the photograph (marked by an arrow); 2B. Cross-sections of fragments of adult last (living chamber) and penultimate whorls. Their almost undeformed umbilical walls preserved on the right are characteristically straight and separated from the evenly arched ventral region (i.e. venter and flank combined) by angular umbilical shoulders. The position of the mid-venter of the last whorl is marked by a black arrow at its upper left. The left flank and umbilical wall of the penultimate whorl are caved in while those of the last whorl are broken off.

Figure 3. *Siberiptychites* (*Siberiptychites*) *stubendorffi* (Schmidt, 1872). GSC 77116. GSC loc. 91310. The same specimen as in Pl. 44, fig. 3 and Pl. 54, fig. 1. Partly preserved terminal cross-section of the specimen and ventral view of the early half of the whorl, x 1.


2A
1
3
2B